TAIL-LENGTH DIFFERENCES IN SNAKES, WITH NOTES ON SEXUAL DIMORPHISM AND THE COEFFICIENT OF DIVERGENCE

Introduction

In the course of certain studies of herpetological correlations the proportionate tail lengths of snakes were investigated. This led to a detour of such extent that it is deemed advisable, in the interest of clarity and balanced treatment, to offer this discussion of tail length separately. At the same time it appears opportune to give examples of the use of the coefficient of divergence as a measure of sexual dimorphism or ontogenetic differentiation.

The tail-length ratios of snakes often prove useful in diagnosis and systematics. The proportion seems to be a rather stable character, so that when differences between related forms do appear, they are likely to be of importance. However, it is a character with respect to which the determination of the significance of differences is not simple. In contrast with characters of lepidosis, which are subject to individual and territorial variations, and sometimes sexual dimorphism, the tail ratio has all of these and usually an ontogenetic variation as well, that is, a change in the ratio of the tail length to the length of body as a snake grows.

As is always the case when comparisons are to be made, we must make sure that our samples—that is, the groups of specimens to be compared—are homogeneous. Thus, if we are comparing two series with respect to a character in which sexual dimorphism is present, and we fail to treat the sexes separately, we may find an apparent difference which really results from an accidental sexual unbalance in the samples, rather than a true difference between the forms being compared. And so, as it will be shown later that tail length is ontogenetically variable in most species of snakes, complete homogeneity can only be secured if we limit our samples to specimens of uniform age. The virtual impossibility of obtaining adequate series under such a restriction renders it necessary to make special statistical provisions for combining specimens of diverse ages. Failure to take this ontogenetic variation into consideration in making species comparisons may lead to false conclusions. It is the purpose of this paper to discuss methods of combining specimens, and to show the extent of ontogenetic variation in several example species. Methods of evaluating differences are developed. Sexual dimorphism is treated.

Statistical Formulas

Problems such as those of tail proportionality, its variation within a homogeneous series of specimens, and differences between series, are sub-

ject to both analytic and graphic attack. If the results are to be trustworthy both methods are usually advisable, since they supplement each other in affording an understanding of the nature of the variation involved.

Where, as in the present case, a preliminary survey of the most superficial nature indicates that ontogenetic variation is probably present, the problem becomes one of correlation—the correlation of tail length proportionality with age. This is not to say that the coefficient of correlation necessarily affords the best measure of the concomitant relationship; on the contrary, in most morphological surveys of this kind, where the correlation between a body part and the whole body, or between two body parts is under investigation, the correlation is sure to be high. In such cases the direction of the regression line, and the extent and nature of the scatter of the individual specimens about that line, will be of greater interest and importance than the numerical value of the correlation coefficient.

The methods of calculating coefficients of correlation, of determining regression lines and errors of estimate, will be found fully detailed in every text book of statistical methods, and therefore will not be discussed here. However, certain formulas involving the relationship between two parts and a whole—the body length, tail length, and length over-all of a snake, for example—are not so readily available, or, if given in a text, may be in a form not directly applicable to the present problem. These formulas are therefore given here, although it should be understood that they involve no originality whatever.

The symbols I shall use are as follows: L, B, T, represent length over-all, body, and tail lengths, respectively. Thus, in each specimen, $L = B + T$.

M_L, M_B, M_T are the sample means of the same quantities, and σ_L, σ_B, σ_T their standard deviations; while σ_{ML}, σ_{MB} and σ_{MT} are the corresponding standard errors of the means. $\sigma_{T.B}$ and $\sigma_{T.L}$ are the standard errors of estimate of T on B or L; r_{TB} and r_{TL} are the corresponding coefficients of correlation. V with any suffix represents a coefficient of variation; N the number of specimens comprising a sample.

$T = a + bL$ and $T = a' + b'B$ are the statements of the linear regression equations which will be discussed, a and a' being the regression constants and b and b' the regression coefficients.

CD is a statistic to which I refer as the coefficient of divergence, defined as the difference between two means divided by half their sum, that is,

$$CD = (M_X - M_Y) \, / \, \tfrac{1}{2} \, (M_X + M_Y),$$

or, if expressed as a percentage,

$$CD\% = 200 \, (M_X - M_Y) \, / \, (M_X + M_Y).$$

σ_{CD} is the standard error of CD.

In most taxonomic work we are accustomed to measuring the lengths of snakes over-all (L) and the tail lengths (T). The length of the body (B) is not generally recorded. It is possible, without the necessity of making the subtraction for each specimen, to calculate the statistics of B, if the statistics of L and T, including their correlation, are available.[1]

We have, first, the two fundamental equations giving the variances (standard deviations squared) of sums and differences:

$$\sigma_L{}^2 = \sigma_T{}^2 + \sigma_B{}^2 + 2\sigma_B\,\sigma_T\,r_{TB}$$

and

$$\sigma_B{}^2 = \sigma_L{}^2 + \sigma_T{}^2 - 2\sigma_L\,\sigma_T\,r_{TL}$$

It will be observed that each equation contains four quantities; if any three be known, the other two in both equations can be readily computed. The second equation can be revised to give the value of the variance of T instead of B by merely interchanging the T's and B's throughout. Thus, any variance can be found if we have the other two and their correlation.

Any correlation coefficient may be derived from another, and the several standard deviations, by the equations:

$$r_{TL} = (\sigma_B\,r_{TB} + \sigma_T)\,/\,\sigma_L$$

and

$$r_{TB} = (\sigma_L\,r_{TL} - \sigma_T)\,/\,\sigma_B$$

Or, the correlations can be found directly from the three variances, from the following equations:

$$r_{TL} = (\sigma_L{}^2 + \sigma_T{}^2 - \sigma_B{}^2)\,/\,2\sigma_L\,\sigma_T$$

and

$$r_{TB} = (\sigma_L{}^2 - \sigma_T{}^2 - \sigma_B{}^2)\,/\,2\sigma_B\,\sigma_T$$

This form will sometimes be convenient when it is desired to avoid the preparation of a correlation table. Again, the T's and B's can be interchanged in the first equation of each pair, if it be desired to ascertain the value of r_{BL} instead of r_{TL}.

Another formula useful in problems dealing with the tail-length ratio is that which permits one to compute the mean of the individual ratios $T\,/\,L$ or $T\,/\,B$ without actually making the division for each specimen.[2] Occasionally approximate values of these ratios are derived by dividing the mean of the tails by the mean of the total lengths, but a result so

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[1] While the six equations which follow are stated in terms of the particular parts B and T, and the whole, L, they are, of course, equally suitable for any items comprising two parts and their sum.

[2] The formulas are from Dahlberg, pp. 94 and 200; also see Pearl, p. 370.

calculated may be somewhat in error. A more accurate value is given by the formula

$$M_{T/L} = \frac{M_T}{M_L} \left[1 - r_{TL} \frac{\sigma_T \sigma_L}{M_T M_L} + \frac{\sigma_L^2}{M_L^2} \right]$$

The standard error of this ratio is

$$\sigma_{T/L} = \frac{M_T}{M_L} \left[\frac{\sigma_T^2}{M_T^2} - 2r_{TL} \frac{\sigma_T \sigma_L}{M_T M_L} + \frac{\sigma_L^2}{M_L^2} \right]^{\frac{1}{2}}$$

If one prefers to work with T / B instead of T / L, it is only necessary to substitute B for L throughout both equations, for they are not restricted to a part and a whole as were those previously given. If it is not desired to calculate r_{TL}, the following substitution may be made in the middle term of the right hand member of either equation:

$$r_{TL}\, \sigma_T\, \sigma_L = (\sigma_L^2 + \sigma_T^2 - \sigma_B^2) / 2$$

It has been shown in these equations how the standard deviation of the body length (σ_B), the correlation between the body length and the length of the tail (r_{TB}), and the mean ratio of the tail to body length, may be computed, even though all of the original measurements may have been recorded in terms of length over-all (L) and tail length (T), and this without the necessity of calculating the value of the body length (B) of each individual specimen, by subtracting T from L. I should also point out that the constants of the regression equation of T on B can be obtained from these data without the necessity of setting up a correlation table of T and B, for

$$b' = r_{TB}\, \sigma_T\, /\, \sigma_B,$$
$$M_B = M_L - M_T$$
and
$$a' = M_T - b' M_B$$

or the form $b' = (\sigma_L^2 - \sigma_T^2)\, /\, 2\sigma_B^2 - \frac{1}{2}$ may be used. These equations involve only factors derived directly from the original statistics of T and L, or which can be determined by the use of the equations already given.

If the relationship between T and L is linear, that between T and B will likewise be linear. Further, if there is a constant term in the T on L equation, there must also be one in the T on B equation, provided the correlation is high. The latter statement is equivalent to saying that if the ratio of the tail length to length over-all changes as a snake grows, then the ratio of the tail length to body length does likewise.

If the correlation r_{TL} is quite high, approximations to the regression constants of the T on B equation may be had directly from the following:

$$a' = a / (1 - b)$$

and

$$b' = b / (1 - b)$$

With respect to the coefficient of divergence, its use will be enhanced if we know its standard error. In problems involving large samples, when determining the significance of the difference between two means, $M_X - M_Y$, it is satisfactory to compute the ratio of this difference to its standard error $(\sigma_{MX}^2 + \sigma_{MY}^2)^{1/2}$, and then find the resulting significance in a table of areas under the normal curve. Thus, to determine the significance of such a difference, when stated in terms of the coefficient of divergence, it should be satisfactory to divide $(\sigma_{MX}^2 + \sigma_{MY}^2)^{1/2}$ by $\frac{1}{2}(M_X + M_Y)$ which will thus leave the significance of the difference unchanged. Hence one might consider $(\sigma_{MX}^2 + \sigma_{MY}^2)^{1/2} / \frac{1}{2}(M_X + M_Y)$ to be an approximate value of the standard error of CD. However, I have calculated the standard error to be as follows:

$$\sigma_{CD} = (M_Y^2\, \sigma_{MX}^2 + M_X^2 \sigma_{MY}^2)^{1/2} / (M_X + M_Y)^2$$

Another expression for the same value is

$$\sigma_{CD} = \frac{(\sigma_{MX}^2 + \sigma_{MY}^2)^{1/2}}{\frac{1}{2}(M_X + M_Y)} \left[1 - 2\, \frac{(M_X - M_Y)(\sigma_{MX}^2 - \sigma_{MY}^2)}{(M_X + M_Y)(\sigma_{MX}^2 + \sigma_{MY}^2)} + \frac{(M_X - M_Y)^2}{(M_X + M_Y)^2} \right]^{1/2}$$

In this second form the relationship with the approximate value first given above may be seen. Since the middle term under the second radical is slightly greater than the third, this presumably[3] more accurate value of the standard error is somewhat lower than the approximation and will therefore give a slightly higher significance. Thus, the approximation is on the safe side.

Spurious Correlation

While the correlation coefficient r_{TL} is useful in computation, it should not be taken as an indication of the relationship between T and L, since it involves a form of spurious correlation. For it is obvious that if a part be larger than normal, the larger part plus a normal remainder will be larger than normal, and hence the total will also be larger than normal. This type of spurious correlation between a part and a whole sometimes vitiates the values of the correlation coefficient which have been presented

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[3] I used the word "presumably" advisedly. I am not as sure of this derivation as I should like to be. It was determined by substituting, in the formula for the standard error of an index, the standard errors of two uncorrelated variables M_X and M_Y. However, $M_X - M_Y$ and $M_X + M_Y$ are correlated and recognition was given this fact. I had expected to find the standard error somewhat higher than the approximation, instead of lower as it worked out.

in biological studies. It is of little importance when the part under consideration is relatively small, as, for example, in the case of snake heads; however, it cannot be neglected in discussing snake tails (except in the case of short-tailed forms like most of the rattlers), particularly in limited-age groups, where the correlation will be lower than in a sample representing all ages.

The trend and extent of spurious correlation may be judged from the fourth equation on page 7. It can be seen that, if the tail is very short in comparison with the body, σ_L / σ_B approaches 1, and σ_T / σ_B approaches zero, so that r_{TB} is almost equal to r_{TL}. This is a verification of the statement with respect to the head lengths of snakes.

The following examples will serve to illustrate some quantitative effects of spurious correlation. In 267 adult female specimens of the Platteville series[4] of *C. v. viridis*, the coefficient of correlation between head and length over-all is 0.906. This involves some spurious correlation, but it is almost negligible, for the correlation between head and body is found, by the use of the equations set forth above, to be 0.899. Similarly, the correlation between the tail length and the length over-all in 102 female Platteville juvenile *C. v. viridis* is 0.702; the corresponding coefficient for tail and body is 0.655. Here the difference is somewhat greater, not only because the tail is proportionately longer than the head, and has a higher variance, but because the initial correlation (0.702) is lower. For the extent of the spurious correlation is affected by the relative sizes of the standard deviations of the parts, and the gross correlation between either part and the whole. Assuming substantially equal coefficients of variation of the parts, the extent of the spurious correlation is greater, the greater a part may be proportional to the whole; but is less the higher the true correlation. Thus, in 28 female specimens (all ages) of *Masticophis flagellum piceus*, from Cape San Lucas, the correlation of the tail to length over-all is 0.990, and the tail to body correlation is reduced only to 0.987; and this, notwithstanding the proportionately long tail as compared to the tail of the rattlesnakes, because the true correlation is very high anyway. The adults of the same series, with a tail to length over-all correlation of 0.924, have a tail to body correlation 0.869, showing a greater difference because of the lower true correlation. In 142 specimens of *Pituophis c. annectens* from western San Diego County, the correlation between the blotches on the body and the entire number from head to tip of tail is 0.962; but if the spurious correlation thus involved be removed, the remaining correlation between the blotches on the body and those on the tail is reduced to 0.637. Here it will be noted the spurious correlation has been given in terms of the larger part; that is, the pro-

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[4] This and other series which have been employed in previous studies, will be found described in Occ. Pap. No. 1, San Diego Soc. Nat. Hist., p. 2, 1936. Similar territorial designations for other collections of specimens will be used in this discussion.

portion of the part to the whole is greater than in the other examples. Hence, the spurious difference is greater, even though the unadjusted or crude correlation is relatively high.

THE COEFFICIENT OF DIVERGENCE AS A MEASURE OF SEXUAL DIMORPHISM IN SCUTELLATION

The coefficient of divergence is a useful statistic for evaluating differences, since it places them on a common basis of comparison, independent of the unit used in measuring any particular character, or the numerical values involved. For example, we may find that the females of one snake species average 10 more ventrals than the males, while those of a second species have an average sexual difference of only 5. But the true relative importance of the sexual dimorphism may not be as 10 to 5, for a single ventral may be of greater importance in the one case than the other. If the males in the first species average 200 ventrals and those of the second 100, then the females would have 5 per cent more in both cases, and the extent of the sexual dimorphism might thus be considered equal in the two cases. The percentage difference in the two cases may indeed be used as a measure of a difference of this type. However, I consider the coefficient of divergence, which is the ratio of the difference between the means to the average of the means, instead of the ratio of the difference to only one of the measurements, to be a better balanced statistic. It is equally useful in comparing the extent of the differences shown by two separate characters within a single species, as, for example, sexual dimorphism in ventral and subcaudal scales, or characters not measurable in the same units, such as ventral scales and body blotches.

On page 9 I have given an equation for determining the standard error of this coefficient. Where the numbers of specimens in the samples to be compared are relatively large, I think a statement of the coefficient, plus and minus three times its standard error, will afford a good indication of the range within which the population coefficient of divergence would probably fall. I realize that this is not at present recognized as an approved method of stating such confidence limits.

Before applying the coefficient of divergence to the measure of sexual dimorphism in tail proportions, I wish to illustrate its use in the measure of simpler differences, that is, differences in characters not ontogenetically variable. I shall first employ it as a measure of sexual dimorphism in scutellation in several homogeneous series of rattlesnakes. As is always the case in such studies, homogeneity is necessary to avoid pseudo-differences resulting from an unbalanced territorial representation in the two samples being compared. For example, if we take widespread samples of *C. cinereous* and a considerable majority of the males happen to come from Arizona, while most of the females are from Texas, an erroneously low figure for the sexual dimorphism would result, since both sexes have more ventrals

in Arizona than Texas. On the other hand, if most of the males happen to be from Texas and the females from farther west, the result would be too high.

TABLE 1

Extent of Sexual Dimorphism in Homogeneous Series of Rattlesnakes In Terms of the Coefficient of Divergence in Per Cent.

Species	Series	Ventrals	Subcaudals	Tail Rings
C. basiliscus	Mexico	− 2.61 ∓ 0.41	21.03 ∓ 1.54	25.91 ∓ 3.19
C. enyo	S. Lower California	− 3.33 ∓ 0.53	26.07 ∓ 1.69	28.58 ∓ 6.20
C. m. molossus	Arizona	− 2.51 ∓ 0.52	16.13 ∓ 1.47	*
C. m. nigrescens	Mexico	− 2.17 ∓ 0.35	20.66 ∓ 1.28	32.28 ∓ 2.67
C. adamanteus	Florida	− 3.64 ∓ 0.38	20.00 ∓ 1.63	36.64 ∓ 5.12
C. cinereous	Arizona	− 1.46 ∓ 0.27	22.57 ∓ 0.97	20.37 ∓ 2.18
C. cinereous	San Patricio	− 0.95 ∓ 0.29	26.96 ∓ 1.06	31.03 ∓ 2.14
C. tortugensis	Tortuga Island	− 0.97 ∓ 0.35	25.35 ∓ 2.54	20.08 ∓ 6.06
C. lucasensis	Cape San Lucas	− 2.11 ∓ 0.24	21.57 ∓ 0.67	19.51 ∓ 1.45
C. ruber	San Diego County	− 1.61 ∓ 0.24	19.39 ∓ 1.11	22.20 ∓ 2.20
C. scutulatus	Arizona	− 1.41 ∓ 0.28	26.22 ∓ 0.98	31.40 ∓ 2.18
C. v. viridis	Platteville	− 3.80 ∓ 0.12	25.12 ∓ 0.45	26.49 ∓ 1.36
C. v. viridis	Pierre	− 4.03 ∓ 0.14	26.16 ∓ 0.47	29.83 ∓ 1.08
C. v. nuntius	Winslow	− 2.98 ∓ 0.36	29.26 ∓ 1.32	24.20 ∓ 2.44
C. v. lutosus	Utah	− 2.62 ∓ 0.36	20.29 ∓ 1.25	23.61 ∓ 2.52
C. v. oreganus	Pateros	− 2.65 ∓ 0.15	19.82 ∓ 0.56	20.67 ∓ 1.14
C. v. oreganus	San Diego County	− 2.70 ∓ 0.15	21.01 ∓ 0.60	26.08 ∓ 1.52
C. m. pyrrhus	San Diego County	− 0.62 ∓ 0.35	21.60 ∓ 1.57	23.56 ∓ 3.21
C. cerastes	Colorado Desert	− 2.42 ∓ 0.27	24.28 ∓ 0.77	24.55 ∓ 2.05
C. l. klauberi	Arizona	− 0.81 ∓ 0.42	21.43 ∓ 1.18	12.32 ∓ 4.50
C. t. pricei	Arizona	− 3.06 ∓ 0.55	15.45 ∓ 1.54	13.48 ∓ 4.50

* Absent, or not clear enough to count. A negative value of the coefficient means that the females exceed the males. The use of the ∓ sign throughout this paper indicates that the following figure is the standard, rather than the probable, error.

Table 1 sets forth the sexual dimorphism of several series of rattlesnakes in terms of the coefficient of divergence and its standard error, in three characters in which the sex differences are known to be considerable, that is, ventrals, subcaudals, and tail rings. Table 2 presents similar data on four characters in which the sexes are usually assumed to be the same, these being scale rows, supralabials, infralabials, and body blotches. In cases where the males are higher, the coefficient is considered to be positive, while it is negative where the females are greater. In the second table, in order to simplify the statement of the coefficient, I have merely indicated by asterisks whether the sexual difference is significant, instead of giving the standard error.

TABLE 2

Extent of Sexual Dimorphism in Homogeneous Series of Rattlesnakes
In Terms of the Coefficient of Divergence in Per Cent.

Species	Series	Scale Rows	Supra-labials	Infra-labials	Body Blotches
C. cinereous	Arizona	1.06*	− 0.42	1.20*	0.34
C. lucasensis	Cape San Lucas	− 1.05*	− 1.03*	0.63	1.54
C. ruber	San Diego County	− 0.23	− 1.43**	− 0.40	1.82*
C. scutulatus	Arizona	− 0.26	0.02	1.38**	0.85
C. v. viridis	Platteville	0.53*	1.64**	0.68*	− 1.62**
C. v. viridis	Pierre	− 0.11	1.12**	1.04**	− 0.11
C. v. oreganus	San Diego County	− 0.51	1.03**	0.28	− 1.02
C. cerastes	Colorado Desert	− 0.83	− 0.37	− 2.02*	− 0.39

* Significant (5 per cent level or below); ** highly significant (1 per cent level or below).

It will be observed that the sexual dimorphism in the ventrals is always negative—that is, the females exceed the males—the extent varying from somewhat above ½ per cent to 4 per cent. The divergence in both subcaudals and tail rings is positive and much higher, running from 16 to over 30 per cent. There is evident a considerable degree of generic uniformity; and some of the related subspecies or species have fairly consistent divergences. All coefficients are highly significant, that is, the ratio of each difference to its standard error is above 2.58 (the 1 per cent significance level) except the ventral differences in *pyrrhus* and *klauberi*, which do not quite reach the 5 per cent level.

The sexual dimorphism shown by the other four characters presented in Table 2 is much less consistent. In only half the cases tested is the sexual dimorphism significant; in 5 instances the result is highly significant. It is probable that there is a slight tendency of the females to have more scale rows than the males, such being the case in six out of eight samples. While not evident in the rattlesnakes, marked sexual dimorphism in scale rows is by no means unknown among snakes. For example, in the sea snakes *Lapemis hardwickii* from Manila Bay the coefficient of divergence in scale rows at mid-body, deduced from 23 males and 31 females,[5] is 12.6 per cent and is highly significant. Do Amaral[6] lists the mid-body counts of 94 males and 116 females of *Bothrops alternata*, from which the coefficient of divergence is found to be 7.7 per cent, the females, as usual, having a higher number of rows. Miss Cochran has shown[7] that,

[5] The counts were made by the late Dr. J. C. Thompson and were received through the courtesy of Mr. J. R. Slevin.

[6] Mem. Inst. Butantan, Vol. 8, p. 178, 1934.

[7] Bull. 117, U.S.N.M., p. 330, 1941.

in the species of the genus *Uromacer* found in Hispaniola, the males almost universally have 11 scale rows at the base of the tail and the females 13. This indicates a coefficient of divergence of nearly 17 per cent.

But in the rattlers these differences do not exceed one percent. Table 2 shows the sexual differences in labials and body blotches to be quite variable, both in nature and extent, the highest being just above 2 per cent in *cerastes* infralabials.

Of course there is nothing novel in the statement that male rattlesnakes have fewer ventrals and more subcaudals than females; these facts have been evident since the earliest studies of the genus were made. These data are only presented to show how the coefficient of divergence can be used as a measure of the extent of these differences; or to express them in numerical terms, so that relative differences between species can be evaluated. Thus we can say that *adamanteus* shows a higher sexual dimorphism in ventral scales than *cinereous,* and that *pricei* is unusually low (compared to most other rattlesnakes) in the extent of the sexual dimorphism in subcaudal scales. Further we are able to say that in *adamanteus* sexual dimorphism is more evident in subcaudals than in ventrals, and is higher in tail rings than either ventrals or subcaudals.

TABLE 3

Extent of Sexual Dimorphism in Homogeneous Series of Snakes In Terms of the Coefficient of Divergence in Per Cent.

Species	Series or Locality	Ventrals	Subcaudals
Adelphicos q. sargii	Volcan Zunil	-7.99 ∓ 0.42	13.40 ∓ 1.61
Geophis nasalis	Volcan Zunil	-2.61 ∓ 0.28	20.92 ∓ 0.75
Aspidura guentheri	Ceylon	-4.52 ∓ 0.38	20.51 ∓ 1.18
Uromacer catesbeyi	Hispaniola	5.52 ∓ 0.67	1.03 ∓ 0.47
Diadophis a. similis	San Diego Bay Area	-5.57 ∓ 0.25	9.28 ∓ 0.68
Phyllorhynchus d. perkinsi	Borego Area	-7.58 ∓ 0.19	25.41 ∓ 0.60
Arizona e. occidentalis	Desert San Diego Co.	-5.15 ∓ 0.51	8.90 ∓ 0.90
Pituophis c. annectens	San Diego County	-2.14 ∓ 0.26	9.30 ∓ 0.69
Lampropeltis g. californiae	San Diego County	-0.79 ∓ 0.36	7.80 ∓ 0.87
Sonora m. linearis	Laguna Island	-6.73 ∓ 0.38	12.37 ∓ 1.00
Sonora o. annulata	San Diego County	-6.05 ∓ 0.31	12.49 ∓ 0.81
Thamnophis o. ordinoides	W. Oregon	1.06 ∓ 0.35	12.48 ∓ 0.64
Thamnophis hammondii	San Diego County	4.17 ∓ 0.20	10.94 ∓ 0.32
Thamnophis radix	Cook County, Ill.	4.01 ∓ 0.36	12.24 ∓ 0.71
Hypsiglena ochrorhynchus	San Diego County	-3.22 ∓ 0.58	15.10 ∓ 1.29
Micrurus n. nigrocinctus	Panama and C. Z.	-7.79 ∓ 0.38	28.42 ∓ 0.95
Micrurus n. divaricatus	Honduras	-6.24 ∓ 0.41	27.89 ∓ 1.13

Table 3 presents data on the ventral and subcaudal sexual divergence of a number of snakes other than rattlers. Again we note the superiority of the females in ventrals, except in certain genera such as *Uromacer* and *Thamnophis;* also that divergence is usually greater in subcaudals than ventrals; and that sexual dimorphism in subcaudals tends to be greater in short-tailed than in long-tailed species.

TABLE 4

Extent of Racial Dimorphism in Homogeneous Series of *Crotalus viridis* In Terms of the Coefficient of Divergence in Per Cent.
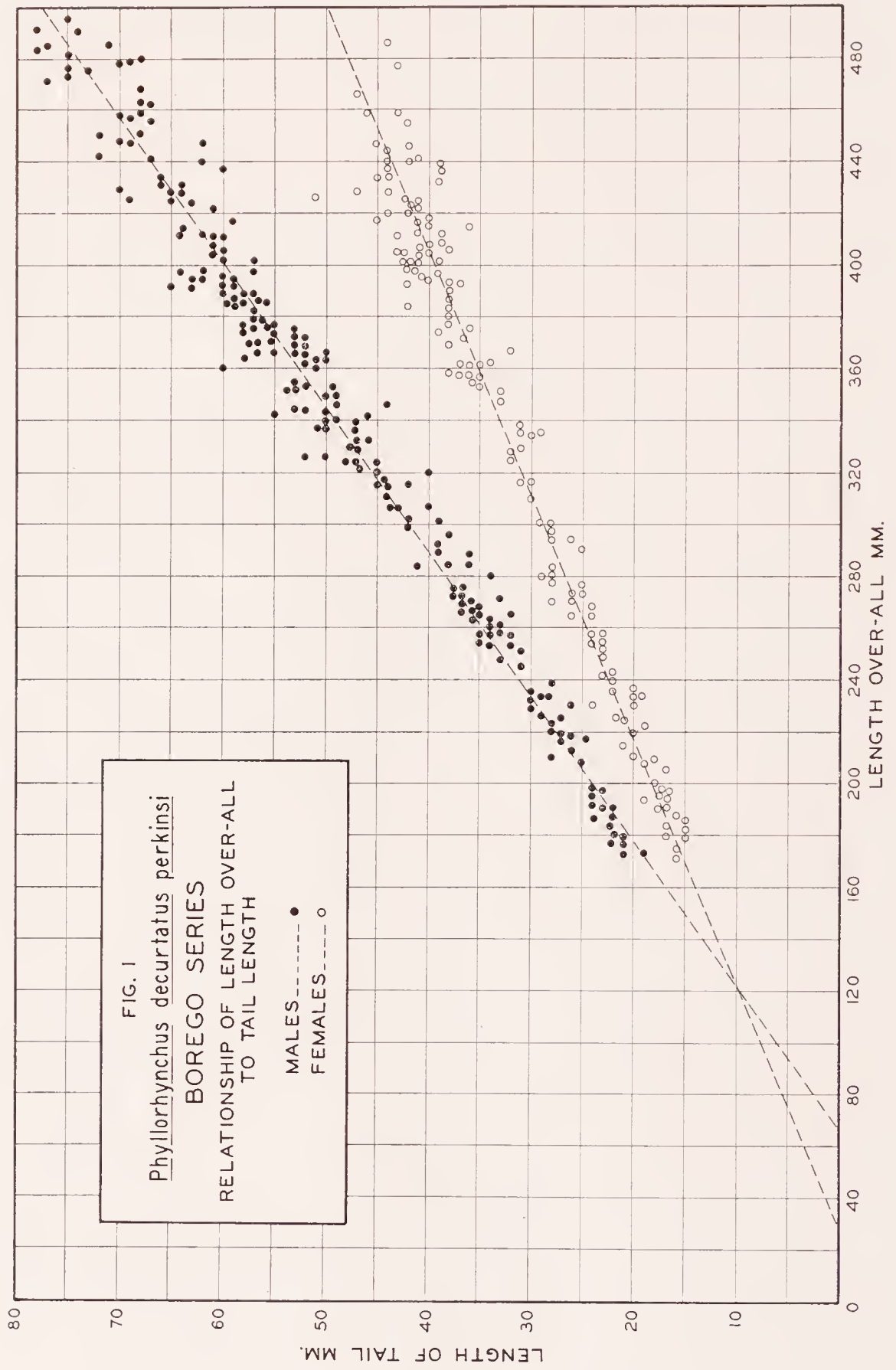
Character	Difference between Platteville and New Mexico Specimens	Difference between Platteville and *Nuntius* Specimens
Scale rows	3.50**	8.81**
Ventrals, males	2.55**	4.36**
Ventrals, females	2.92**	5.07**
Subcaudals, males	1.98*	5.02**
Subcaudals, females	1.96	9.00**
Supralabials	− 0.55	0.00
Infralabials	0.25	3.31**
Body blotches	5.04**	1.88*
Tail rings, males	2.26	2.81*
Tail rings, females	3.79	3.96

* Significant (5 per cent level); ** highly significant (1 per cent level).

In Table 4 the coefficient of divergence has been employed as a measure of territorial variations or clines. Here are shown, first, the differences between the Platteville series of *Crotalus v. viridis* from northeastern Colorado and the same subspecies in New Mexico; and secondly the differences between the Platteville specimens and *C. v. nuntius* from northeastern Arizona, which intergrades with *C. v. viridis* along the Arizona-New Mexico border. It will be observed that the more important characters—scale rows, ventrals, and subcaudals—show an increasing difference with wider territorial separation; but this trend is not manifest in all characters.

METHODS AND PRECAUTIONS IN TAIL-LENGTH STUDIES

If a morphological character such as tail-length proportionality is to be thoroughly investigated, a graphical approach is to be strongly recommended, even though the final determination of the regression equation be by analytical methods. By graphical is meant the plotting of each specimen on rectangular co-ordinate paper with lengths over-all (or body lengths) along the horizontal scale and tail lengths on the vertical (Fig. 1).

FIG. I
Phyllorhynchus decurtatus perkinsi
BOREGO SERIES
RELATIONSHIP OF LENGTH OVER-ALL
TO TAIL LENGTH

MALES ------- •
FEMALES ----- o

The scales should be so arranged that the origin is in evidence; that is, even if no snakes of the species being investigated are below 300 mm. in length, do not begin the bottom scale at 300, but at zero. By so doing it will be possible to check the regression formula by noting the points of intersection with the axes. In plotting specimens the use of different symbols for the sexes is to be recommended; if specimens from different districts are to be compared, colors may be employed to advantage. However, if the fit of regression lines to the primary data is to be studied, it will not be found advisable to plot too many series on a single sheet.

This graphical method of attack is virtually imperative, even though followed by a complete correlation study, since it will give a necessary picture of the general relationship. It will indicate at once whether sufficient curvature is in evidence in a trend line to warrant a test for linearity. It will give an idea of the extent of sexual dimorphism, and also of territorial differences. While not determining the significance of the constant term (a) in the regression equation, it will at least indicate its relative importance and whether it is at all safe to consider the tail-length ratio ontogenetically constant. It will afford a good idea of the nature and extent of the scatter of the individual specimens about the regression line. Aberrant specimens will stand out conspicuously; these may then be given further study to find whether they may not result from inaccurate sexing, incomplete tails, inaccurate measurements, mistakes in recording, or other errors, as will not infrequently be found to be the case. And even though these non-conformists prove to be true aberrants, it may be desirable to give consideration to their elimination from the data used in the regression computation. While this may seem a questionable or non-scientific procedure, it is often advisable; for a single badly distorted or freakish specimen can considerably affect the determinations, particularly if the sample be relatively small; and it is to be remembered that what we seek is the mode (using the word in its non-technical sense) of the normal population, uncomplicated by freaks.

The graphical set-up is also useful in checking the accuracy of the constants of the regression equation, as determined by the subsequent calculations.

If it be desired to depend entirely on a graphic determination of the regression line, a procedure requiring only a minor fraction of the time needed for an analytical study, the use of a black thread, rather than a straightedge, is to be recommended. One end of the thread should be fastened to the back edge of the table or drawing board; the other end, to which a small weight is attached, is allowed to dangle over the near edge. Then the sheet containing the plot of the specimens may be manipulated under the thread until what seems to be the best fit is obtained. The co-ordinates (T_1 and L_1; T_2 and L_2) of any two points on the line (pref-

erably near opposite ends) are recorded. The required equation $T = a + bL$ may then be determined from the following:

$$a = (T_1 L_2 - T_2 L_1) / (L_2 - L_1) \text{ and } b = (T_2 - T_1) / (L_2 - L_1)$$

Values of B may be substituted for values of L if one prefers working with body length instead of length over-all. The calculations will be simplified if one of the points be selected on an axis, so that either T_1 or L_1 become zero.

With some practice, particularly if the dispersion about the regression line is moderate in extent, and there is a fairly even ontogenetic distribution of the specimens, a quite accurate determination of the regression line can be obtained by this simple method. In placing the line, it is well to remember to balance vertical deviations on each side of the line against each other, rather than deviations perpendicular to the line. If this be not done, a tendency will be noted whereby the graphically determined line will have a slightly steeper slope than a line found by the least-squares or analytical method.

A still more accurate placing of the regression line may be secured by totaling the lengths over-all (or body lengths) and the lengths of the tails, and dividing by the number of specimens, thus securing the values of M_L and M_T. These values give the co-ordinates of a point through which the regression line should be made to pass. Or the juvenile and adult means may be determined separately and the line passed through the two points thus located.

In an analytical determination, in computing the values of M_T and M_B, and the standard deviations, no specimen should be included in calculating one statistic unless it be available for all. For this reason, even though values of B, rather than L, may be used, no specimen with an incomplete tail should be tabulated.

The determination of boundary lines between the sexes will be found discussed on page 56.

Incomplete tails are particularly prevalent in attenuated forms; this is complicated in some species by the absence of a characteristic terminal cone,[8] which makes it almost impossible to determine whether the tail really is complete. Such is the case, for example, in *Masticophis flagellum.* There is some evidence from examinations of broods that certain species of snakes normally lose the tips of their tails shortly after birth, possibly in the course of shedding. Also, it seems as if some snakes are able to regenerate a tail tip in a manner which makes it quite difficult to ascertain whether the tail is complete.

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[8] In some forms the presence of a prominent terminal cone, containing a rather characteristic longitudinal crease, makes the determination quite definite.

Errors in sexing should be minimized; obviously they will tend to reduce the true extent of sexual dimorphism. They are likely to occur most frequently among the juveniles, yet the juveniles cannot be omitted if accurate regression lines are to be obtained.

A graphic set-up of the ventral-subcaudal relationship will often substantiate tail-length discrepancies in certain specimens—that is, the same specimens will be found to deviate from the mode in both plots, thus clearly indicating those which should be the subject of a re-examination. While it should not be forgotten that there may be cross-correlation in these characters, so that aberrance in one may be coincident with abnormality in the other, this type of double check will frequently disclose errors of sexing, measurement, or recording.

As we may well suspect the existence of ecological variations, our samples should be limited, as far as possible, to collections from quite restricted localities. However, from the standpoint of accuracy of determination, meaning the adherence of the sample statistics to the true population parameters, an increase in the number of specimens contained in a sample is decidedly beneficial. Therefore, if there is no evidence of territorial variation, it may sometimes be advantageous to employ a larger sample from a less restricted locality.

No definite rule can be laid down with respect to the adequacy of samples for the determination of tail length proportionality, except this: the larger the better, if homogeneity be not sacrificed. One can hardly expect to secure dependable results with less than twenty-five full-tailed specimens of each sex. The accuracy will also depend to an important degree on the ontogenetic scatter of the sample; it is essential that both juveniles and adults be represented in the sample, if an ontogenetically complete and accurate regression line is expected. These terminal individuals tend to pull the line into its proper position; limited-length groups will seldom produce the same, or even a closely approaching equation. The reason for this is not necessarily a general curvature of the regression line, under which circumstances the first degree regression line of a limited-age group would tend to produce a tangent to the complete-age line. Rather it is the greater effect that deviations of individuals from the normal have upon the determination of the regression line when only a limited-age group is included in the study.

There is, in fact, one condition in the method of analysis that to some extent renders a graphical determination superior, or at least makes it important for purposes of comparison. This is the fact that deviations from the regression line (as will subsequently be shown) are approximately proportionate to tail length. Thus adult abnormalities—that is, abnormal deviations from a truly representative regression line—affect the determination of the line to a much greater degree than proportionate deviations in juveniles. Sometimes a single aberrant adult will throw the

line so far out of position that it will clearly not be truly representative of the species, particularly in the juvenile range; this is especially true if there be a single very large adult which is in any way abnormal. Under such circumstances a specimen of this kind should be omitted. In some series where the number of juveniles is inadequate to balance the adults the most satisfactory solution is to duplicate the entry for each juvenile.

This relative ineffectiveness of the juveniles might be compensated for by using the logarithms of the measurements instead of the lengths themselves. However, if the linear relationship includes a constant term, the line is no longer straight when plotted on a logarithmic basis, which complicates the calculations. For this reason I prefer to use the simpler method, but with a close scrutiny of the graphic situation to eliminate any juvenile inadequacies or over-effects of aberrant adults. It should be understood that these modifications are only made when an available series is inadequate in numbers or unbalanced in ontogenetic distribution.

There is also the matter of accuracy and uniformity of measurement. The tail length should be measured to the center, rather than the lower edge, of the anal plate. Attempts to record stiff and contorted specimens should be avoided. Where possible, specimens should be measured when freshly killed, since the data so derived will represent a true natural relationship; furthermore, unhardened specimens may be stretched out along a ruler and thus more accurately measured. However, one is usually dependent on preserved specimens which have already set; in these there will be some differential shrinkage between body and tail, resulting from preservation. This is not likely to prove of importance in taxonomic work unless two series to be compared have been preserved by different methods.

The following data will serve to illustrate the relative shrinkage resulting from preservation in alcohol:

		Shrinkage in per cent	
	Specimens	Body	Tail
Masticophis f. piceus	22	2.76	0.34
Phyllorhynchus d. perkinsi	18	3.15	0.43
Pituophis c. annectens	28	2.09	0.22

It will be observed that the tail suffers almost no shrinkage; it is not unusual for specimens to show a slight increase in length after preservation. It is probable that, on the average, the body shrinkage will not usually exceed 3 per cent, although it will be found to be higher than this figure in young specimens.

Variation of Tail Length Within Homogeneous Populations

Having discussed some of the methods and precautions involved in the utilization of tail length proportionality in taxonomic studies, I shall now illustrate their use with results secured from a variety of species. As is so often the case in evaluating a diagnostic character it is desirable first to ascertain the extent and the nature of the variation of such a character within homogeneous groups, before attempting to discover the degrees of difference between groups or the extent of sexual dimorphism.

Assuming the availability of homogeneous series of snakes, the principal questions to be answered respecting the tail-length ratios are: (1) is the relationship linear, or substantially so? (2) does the ratio of the tail length to total length remain constant, or vary with age? (3) in what manner does the dispersion of individuals about the species regression line change with age?

To answer these questions, 48 species and subspecies of snakes were investigated, the resulting statistics being set forth in Tables 5 to 9, inclusive. However, before the determinations are discussed, it is necessary to supply some descriptive information on the several samples, since they vary considerably in adequacy, and the geographical data cannot be given in the tables, although the numbers of available specimens will be found there.

Lichanura roseofusca roseofusca Cope.

A series fairly well distributed ontogenetically; the specimens are from extreme northern Lower California, and San Diego and southern Riverside counties, in California. Both coastal and desert specimens are included, since there seem to be no important tail-ratio differences. I was rather surprised to find that the scarred and blunt tails, so frequent in the adults of this species, which I had always supposed were mutilated and truncated, are presumably complete, since they fall along a consistent regression line. Evidently, the bluntness must result from internal causes, possibly from the swelling of the anal scent glands, which are very large and odorous in this species.

TABLE 5
Relationship of Tail Length to Length Over-all

Species or Subspecies	Number of Specimens		Coefficient of Correlation, r_{TL}		Regression Coefficient, b		Regression Constant, a		Standard Errors σ_b		σ_a		Standard Error of Estimate		Mean Coefficient of Variation, %	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Lichanura r. roseofusca	43	57	.983	.992	.166	.143	−14.32	−6.15	.0049	.0026	2.94	1.61	6.22	3.75	7.83	4.81
Adelphicos q. sargii	67	62	.984	.971	.162	.121	−2.98	−0.93	.0036	.0039	0.88	0.90	1.56	1.80	5.56	6.84
Geophis brachycephala	25	24	.997	.990	.204	.163	−4.26	−0.28	.0031	.0050	0.70	1.24	1.10	1.36	2.83	3.52
Geophis nasalis	115	87	.980	.976	.199	.147	−6.37	−2.21	.0038	.0036	0.81	0.76	1.96	1.44	5.53	5.10
Diadophis a. similis	133	134	.978	.981	.212	.179	−5.50	−3.59	.0039	.0031	1.10	0.95	2.48	3.08	4.64	6.22
Diadophis p. arnyi I	71	40	.948	.973	.192	.159	−0.28	−0.40	.0077	.0061	1.88	1.47	3.28	2.76	7.24	7.65
Diadophis p. arnyi II	247	183	.983	.974	.210	.164	−4.87	−2.00	.0025	.0028	0.57	0.61	2.27	2.36	5.48	7.32
Boaedon l. lineatus I	23	33	.974	.986	.181	.130	−7.76	−4.36	.0091	.0039	5.59	2.87	7.07	3.95	7.12	4.49
Boaedon l. lineatus II	21	12	.994	.998	.206	.145	−10.60	−3.13	.0050	.0028	2.25	1.50	2.23	1.97	2.81	2.87
Masticophis f. piceus	25	34	.986	.991	.270	.268	−4.69	1.21	.0095	.0065	8.38	6.97	17.86	13.43	8.57	4.95
Masticophis lateralis	23	24	.996	.992	.315	.304	−9.11	−5.40	.0058	.0082	5.20	7.66	7.45	10.02	2.85	3.76
Salvadora g. virgultea	23	23	.996	.995	.237	.230	−2.38	−2.01	.0047	.0049	3.34	3.18	4.72	4.29	2.98	3.02
Phyllorhynchus b. browni	25	12	.960	.966	.161	.084	−7.60	−1.06	.0097	.0072	2.87	2.19	2.54	1.79	6.52	7.50
Phyllorhynchus d. nubilus	8	4	.996	.999	.177	.080	−11.62	0.11	.0062	.0023	1.85	0.66	1.09	0.39	2.75	1.79
Phyllorhynchus d. perkinsi I	214	148	.973	.976	.179	.106	−12.01	−3.41	.0029	.0020	1.02	0.67	3.58	2.15	7.32	6.75
Phyllorhynchus d. perkinsi II	34	16	.991	.957	.182	.107	−12.30	−2.48	.0043	.0087	1.60	2.63	2.25	2.72	4.26	9.44
Arizona e. occidentalis I	50	25	.993	.998	.132	.131	1.85	−5.53	.0023	.0016	1.62	1.28	3.05	1.90	3.36	2.34
Arizona e. occidentalis II	46	12	.990	.995	.143	.133	−2.63	−3.40	.0031	.0041	2.02	2.05	3.36	2.45	3.79	4.23
Pituophis c. annectens	155	144	.993	.991	.165	.148	3.91	4.61	.0016	.0017	1.37	1.20	7.48	6.52	5.58	6.53
Pituophis c. deserticola I	31	23	.994	.995	.127	.120	8.50	5.31	.0026	.0027	2.23	2.39	4.94	4.44	4.59	4.31
Pituophis c. deserticola II	23	15	.990	.994	.148	.144	0.57	−7.35	.0047	.0044	4.50	3.86	6.68	4.87	4.95	4.37
Lampropeltis g. californiae	278	249	.977	.984	.131	.128	3.62	1.73	.0017	.0015	1.05	0.62	8.04	6.41	10.84	8.78
Rhinocheilus l. lecontei I	30	23	.991	.994	.136	.126	3.01	1.77	.0034	.0031	2.10	1.56	3.77	2.74	4.58	4.56
Rhinocheilus l. lecontei II	35	10	.988	.992	.139	.136	1.79	−1.99	.0038	.0062	2.51	3.43	3.68	3.27	4.05	4.70
Rhinocheilus l. clarus	29	13	.987	.983	.146	.145	−1.77	−8.10	.0046	.0081	3.04	4.87	3.62	3.59	3.95	4.68
Toluca l. lineata I	20	29	.995	.982	.212	.148	−2.22	0.00	.0050	.0056	0.99	1.08	1.07	1.41	2.78	5.06
Toluca l. lineata II	39	28	.990	.981	.220	.168	−4.71	−3.10	.0051	.0065	1.04	1.30	1.82	1.92	4.78	6.58
Toluca l. varians	71	69	.993	.979	.221	.161	−3.74	−0.14	.0031	.0041	0.62	0.92	1.71	2.13	4.53	6.22
Sonora m. linearis	43	57	.996	.990	.219	.181	−2.74	0.00	.0030	.0034	0.87	0.74	1.15	1.39	2.64	3.66
Sonora o. occipitalis	39	13	.971	.969	.195	.184	−2.82	−5.61	.0079	.0141	2.24	3.78	1.95	2.43	3.72	5.66
Sonora o. annulata	200	119	.974	.978	.204	.178	−2.92	−2.49	.0034	.0035	0.94	0.94	2.68	2.39	5.04	5.21
Chilomeniscus s. stramineus	22	22	.957	.954	.137	.122	1.83	0.17	.0108	.0086	2.01	1.71	1.13	1.36	4.20	5.66
Thamnophis hammondii	168	153	.994	.995	.246	.220	−0.29	3.56	.0021	.0019	0.87	0.81	4.29	4.45	4.69	5.00
Thamnophis o. ordinoides	74	84	.991	.983	.274	.233	−6.86	−2.67	.0044	.0048	1.56	1.74	2.71	4.37	3.09	5.63
Thamnophis o. biscutatus	107	95	.992	.993	.254	.232	3.97	4.32	.0031	.0028	1.52	1.31	6.28	5.67	5.35	5.51
Conopsis nasus	61	70	.982	.981	.152	.117	−0.17	0.45	.0038	.0028	0.92	0.68	1.79	1.36	5.06	4.92
Hypsiglena ochrorhynchus	55	30	.971	.986	.187	.152	−4.64	−1.19	.0064	.0048	1.88	1.34	2.52	1.82	5.06	4.57
Trimorphodon vandenburghi	22	16	.974	.993	.163	.135	−0.05	3.76	.0085	.0043	4.81	2.64	4.44	4.17	4.90	5.29
Tantilla eiseni	18	15	.995	.992	.263	.251	−4.53	−8.34	.0067	.0090	1.90	2.02	1.67	2.52	2.44	5.63
Elapsoidea niger	15	29	.967	.974	.086	.082	−3.67	−7.43	.0062	.0037	2.34	1.48	1.56	1.43	5.56	5.63
Micrurus a. mayensis	14	16	.977	.976	.161	.115	−7.28	−1.13	.0104	.0077	6.76	4.67	3.57	2.87	3.69	4.24
Micrurus n. nigrocinctus	39	32	.994	.991	.148	.099	−3.99	−0.87	.0028	.0025	1.28	1.45	2.88	3.27	4.51	6.35
Micrurus n. divaricatus	38	28	.996	.995	.162	.105	−6.53	−0.43	.0023	.0021	1.14	1.25	3.06	2.62	4.70	4.65
Agkistrodon m. mokeson	169	131	.973	.976	.122	.120	10.69	7.71	.0022	.0024	1.28	1.24	5.45	4.30	7.12	6.34
Trimeresurus gramineus	24	16	.994	.997	.219	.164	−12.98	0.52	.0053	.0033	2.84	1.40	2.34	1.56	2.29	2.30
Trimeresurus elegans	17	12	.990	.997	.188	.156	−6.55	3.78	.0070	.0035	5.30	2.16	5.90	2.69	4.54	2.71
Bothrops insularis	92	94	.958	.956	.145	.122	2.78	4.34	.0053	.0039	3.68	2.85	3.96	4.88	3.87	5.31
Atheris squamigera	22	25	.965	.977	.195	.154	−13.67	−5.23	.0126	.0070	6.00	3.57	4.72	3.21	6.09	4.43

TABLE 6
Relationship of Tail Length to Body Length

Species or Subspecies	Number of Specimens		Coefficient of Correlation, r_{TB}		Regression Coefficient, b'		Regression Constant, a'		Standard Errors				Standard Error of Estimate		Mean Coefficient of Variation, %	
									$\sigma_{b'}$		$\sigma_{a'}$					
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Lichanura r. roseofusca	43	57	.975	.990	.197	.167	− 16.32	− 6.93	.0070	.0032	2.94	1.61	7.44	4.38	9.37	5.61
Adelphicos q. sargii	67	62	.978	.962	.192	.136	− 3.33	− 0.79	.0051	.0050	0.86	1.03	1.85	2.05	6.60	7.78
Geophis brachycephala	25	24	.996	.985	.256	.193	− 5.28	− 0.14	.0054	.0072	0.98	1.48	1.38	1.62	3.56	4.20
Geophis nasalis	115	87	.969	.966	.246	.171	− 7.42	− 2.27	.0059	.0050	1.05	0.91	2.44	1.71	6.90	6.04
Diadophis a. similis	133	134	.964	.972	.265	.215	− 6.05	− 3.82	.0063	.0045	1.45	1.17	3.14	3.74	5.88	7.57
Diadophis p. arnyi I	71	40	.920	.962	.230	.186	1.15	− 0.01	.0118	.0086	2.32	1.75	4.05	3.27	8.93	9.09
Diadophis p. arnyi II	247	183	.972	.963	.262	.193	− 5.60	− 1.95	.0040	.0040	0.74	0.74	2.87	2.82	6.93	8.74
Boaedon l. lineatus I	23	33	.967	.984	.219	.149	− 8.65	− 4.77	.0126	.0049	6.40	2.52	7.98	4.29	8.04	4.87
Boaedon l. lineatus II	21	12	.991	.998	.259	.170	− 13.01	− 3.62	.0080	.0038	2.92	1.76	2.81	2.31	3.53	3.36
Masticophis f. piceus	25	34	.973	.983	.364	.362	− 3.31	4.19	.0178	.0121	11.51	9.48	24.42	18.32	11.71	6.75
Masticophis lateralis	23	24	.993	.984	.457	.432	− 12.00	− 5.00	.0084	.0170	5.27	11.06	10.89	14.36	4.17	5.39
Salvadora g. virgultea	23	23	.993	.992	.310	.298	− 2.55	− 2.09	.0125	.0124	6.83	6.23	9.59	8.38	6.05	5.89
Phyllorhynchus b. browni	25	12	.943	.959	.188	.091	− 8.14	− 0.91	.0138	.0085	3.51	2.40	3.02	1.96	7.75	8.18
Phyllorhynchus d. nubilus	8	4	.995	.999	.215	.087	− 14.04	0.12	.0092	.0027	2.35	0.72	1.32	0.43	3.35	1.95
Phyllorhynchus d. perkinsi I	214	148	.960	.970	.214	.118	− 13.68	− 3.28	.0043	.0025	1.29	0.76	4.35	2.41	8.91	7.54
Phyllorhynchus d. perkinsi II	34	16	.987	.946	.222	.119	− 14.71	− 2.38	.0065	.0109	2.03	2.97	2.75	3.04	5.20	10.56
Arizona e. occidentalis I	50	25	.990	.998	.151	.151	2.37	− 5.75	.0031	.0021	1.86	1.31	3.50	2.19	3.87	2.69
Arizona e. occidentalis II	46	12	.986	.994	.167	.153	− 5.75	− 2.70	.0042	.0055	2.37	2.37	3.92	2.82	4.43	4.87
Pituophis c. annectens	155	144	.990	.988	.197	.174	5.10	5.76	.0022	.0023	1.63	1.41	8.95	7.66	6.67	7.66
Pituophis c. deserticola I	31	23	.992	.993	.145	.136	9.93	6.19	.0034	.0035	2.53	2.71	5.66	5.08	5.26	4.93
Pituophis c. deserticola II	23	15	.986	.992	.172	.168	1.25	− 8.31	.0064	.0060	5.27	4.54	7.83	5.69	5.80	5.10
Lampropeltis g. californiae	278	249	.969	.979	.149	.145	4.74	2.38	.0023	.0019	1.19	1.05	9.26	7.35	12.48	10.07
Rhinocheilus l. lecontei I	30	23	.988	.992	.157	.144	3.73	2.15	.0045	.0041	2.41	1.75	4.36	3.13	5.29	5.21
Rhinocheilus l. lecontei II	35	10	.984	.989	.161	.157	2.48	− 2.09	.0051	.0083	2.90	3.98	4.27	3.78	4.70	5.44
Rhinocheilus l. clarus	29	13	.982	.977	.170	.168	− 1.56	− 8.89	.0063	.0111	3.57	5.77	4.24	4.20	4.62	5.46
Toluca l. lineata I	20	29	.992	.975	.268	.173	− 2.68	0.22	.0050	.0056	1.27	1.26	1.36	1.65	3.53	5.93
Toluca l. lineata II	39	28	.984	.973	.280	.201	− 5.73	− 3.42	.0084	.0094	1.37	1.59	2.34	2.31	6.12	7.91
Toluca l. varians	71	69	.989	.970	.282	.190	− 4.59	0.18	.0031	.0041	0.81	1.09	2.19	2.54	5.81	7.41
Sonora m. linearis	43	57	.994	.985	.280	.220	− 3.38	0.20	.0079	.0051	1.37	0.90	2.37	1.70	5.43	4.47
Sonora o. occipitalis	39	13	.955	.954	.238	.222	− 2.50	− 5.99	.0079	.0141	2.81	4.73	2.42	2.98	4.62	6.93
Sonora o. annulata	200	119	.959	.967	.252	.214	− 2.69	− 2.44	.0053	.0052	1.20	1.21	3.36	2.91	6.32	6.33
Chilomeniscus s. stramineus	22	22	.941	.940	.156	.136	2.54	0.57	.0125	.0111	1.98	1.94	1.31	1.55	4.86	6.43
Thamnophis hammondii	168	153	.989	.991	.324	.280	0.12	4.89	.0038	.0031	1.15	1.03	5.69	5.69	6.21	6.40
Thamnophis o. ordinoides	74	84	.982	.968	.374	.299	− 8.50	− 2.35	.0084	.0085	2.20	2.37	3.73	5.93	4.25	7.65
Thamnophis o. biscutatus	107	95	.986	.989	.338	.300	6.14	6.13	.0056	.0047	2.02	1.69	8.42	7.37	7.18	7.16
Conopsis nasus	61	70	.975	.975	.178	.132	0.08	0.66	.0053	.0036	1.09	0.76	2.11	1.54	5.97	5.57
Hypsiglena ochrorhynchus	55	30	.955	.981	.227	.178	− 4.75	− 1.17	.0096	.0067	2.35	1.59	3.09	2.14	6.21	5.38
Trimorphodon vandenburghi	22	16	.963	.990	.193	.156	1.08	4.56	.0121	.0058	5.74	3.19	5.30	4.82	5.86	6.12
Tantilla eiseni	18	15	.991	.985	.355	.332	− 5.77	− 10.71	.0123	.0160	2.63	2.81	2.27	3.36	3.31	7.52
Elapsoidea niger	15	29	.961	.969	.093	.089	− 3.79	− 7.92	.0075	.0043	2.59	1.63	1.71	1.56	6.08	6.13
Micrurus a. mayensis	14	16	.967	.970	.190	.130	− 7.58	− 0.78	.0144	.0087	7.96	4.68	4.15	3.24	4.30	4.80
Micrurus n. nigrocinctus	39	32	.992	.988	.173	.110	− 4.50	− 0.84	.0036	.0031	1.52	1.61	3.37	3.63	5.29	7.05
Micrurus n. divaricatus	38	28	.995	.993	.193	.117	− 7.57	− 0.40	.0023	.0021	1.38	1.40	3.66	2.94	5.61	5.22
Agkistrodon m. mokeson	169	131	.965	.969	.137	.136	12.74	9.30	.0029	.0031	1.42	1.39	6.20	4.88	7.12	6.34
Trimeresurus gramineus	24	16	.990	.996	.280	.196	− 16.07	0.71	.0087	.0047	3.75	1.67	3.00	1.87	2.93	2.76
Trimeresurus elegans	17	12	.984	.996	.231	.184	− 7.25	4.59	.0106	.0049	6.59	2.70	7.26	3.19	5.59	3.21
Bothrops insularis	92	94	.943	.943	.167	.137	4.99	6.21	.0062	.0050	3.66	3.21	4.63	5.53	4.53	6.02
Atheris squamigera	22	25	.945	.968	.236	.180	− 14.86	− 5.39	.0194	.0092	7.68	4.03	5.84	3.58	7.54	4.94

TABLE 7

Mean and Limiting Lengths of Specimens Comprising the Samples

Species or Subspecies	Mean Length Over-all		Mean Body Length		Mean Tail Length		Standard Deviations σ_L		σ_B		σ_T		Range of Length Over-all* Minimum		Maximum	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Lichanura r. roseofusca	566.21	586.19	486.79	508.25	79.42	77.95	195.63	210.52	163.36	180.35	32.96	30.43	276-33	284-35	840-110	951-133
Adelphicos q. sargii	191.52	226.11	163.45	199.77	28.07	26.34	53.37	59.71	44.74	52.54	8.79	7.42	90-13	98-12	268-44	335-41
Geophis brachycephala	211.52	239.58	172.64	200.92	38.88	38.67	71.79	56.24	57.15	47.12	14.68	9.24	114-20	127-20	342-66	340-52
Geophis nasalis	209.37	207.03	174.01	178.77	35.37	28.26	48.32	43.32	38.73	36.99	9.83	6.54	106-16	112-14	292-54	283-42
Diadophis a. similis	277.88	296.81	224.54	247.39	53.34	49.43	54.61	86.82	43.11	71.38	11.82	15.81	135-24	121-19	390-79	507-88
Diadophis p. arnyi I	239.56	229.83	192.21	193.80	45.35	36.03	50.62	72.33	41.02	60.93	10.25	11.78	121-24	112-18	322-59	330-51
Diadophis p. arnyi II	220.37	209.64	179.00	177.34	41.37	32.30	57.40	62.39	45.41	52.32	12.25	10.47	112-20	115-17	315-56	361-57
Boaedon l. lineatus I	590.43	712.12	491.26	624.18	99.17	87.94	165.20	178.44	135.32	155.32	30.71	23.45	227-34	252-25	820-140	944-107
Boaedon l. lineatus II	436.76	493.50	357.19	424.83	79.57	68.67	99.15	213.50	78.71	182.45	20.59	31.12	222-37	299-39	557-101	938-133
Masticophis f. piceus	790.40	1009.71	581.92	738.21	208.48	271.50	382.05	359.71	279.56	263.75	104.51	97.19	302-75	306-73	1481-395	1531-384
Masticophis lateralis	858.87	894.38	597.65	627.96	261.22	266.42	275.74	253.35	189.09	176.62	87.09	77.62	343-99	406-117	1218-380	1385-417
Salvadora g. virgultea	678.78	625.70	520.21	483.52	158.57	142.17	214.24	187.83	163.51	144.60	51.00	43.49	315-72	280-60	1027-244	892-200
Phyllorhynchus b. browni	290.08	296.33	251.08	272.41	39.00	23.92	53.36	75.60	44.86	69.25	8.93	6.60	166-18	180-13	362-49	384-32
Phyllorhynchus d. nubilus	288.50	272.50	249.00	250.50	39.50	22.00	65.82	100.02	54.17	91.99	11.71	8.04	194-22	173-14	343-50	408-33
Phyllorhynchus d. perkinsi I	340.34	329.91	291.52	298.01	48.82	31.89	84.20	90.09	69.25	80.55	15.47	9.81	173-19	171-16	495-75	486-44
Phyllorhynchus d. perkinsi II	356.79	292.00	304.03	263.19	52.76	28.81	90.02	80.74	73.64	72.14	16.57	9.04	168-16	190-19	510-82	435-50
Arizona e. occidentalis I	673.98	662.56	583.42	581.16	90.56	81.40	187.52	243.15	162.86	211.24	24.86	31.97	262-34	213-24	1061-133	1063-133
Arizona e. occidentalis II	635.94	462.42	547.44	404.50	88.50	57.92	162.81	179.03	139.52	155.32	23.57	23.85	275-36	245-34	863-124	796-103
Pituophis c. annectens	789.66	642.21	655.63	542.29	134.03	99.92	386.06	325.93	322.53	277.64	64.05	48.80	322-56	322-48	1844-284	1504-210
Pituophis c. deserticola I	783.06	815.26	675.45	712.26	107.61	103.00	346.15	352.12	302.38	309.96	44.08	42.42	415-60	439-57	1495-189	1566-197
Pituophis c. deserticola II	910.48	826.20	775.52	714.53	134.96	111.67	303.92	296.50	259.14	253.83	45.33	42.97	420-60	417-51	1364-187	1194-165
Lampropeltis g. californiae	540.51	559.10	466.33	486.08	74.18	73.01	281.16	276.36	244.59	241.21	37.57	35.81	205-29	210-25	1301-161	1233-143
Rhinocheilus l. lecontei I	583.13	462.57	500.83	402.52	82.30	60.04	206.43	187.30	178.40	163.73	28.31	23.75	202-27	231-31	842-111	740-97
Rhinocheilus l. lecontei II	639.94	526.40	549.09	456.80	90.86	69.60	166.54	176.30	143.40	152.35	23.46	24.17	280-37	273-33	890-121	749-96
Rhinocheilus l. clarus	641.79	586.00	550.03	509.23	91.76	76.77	148.19	127.88	126.65	108.41	21.89	18.84	361-48	343-43	843-120	787-103
Toluca l. lineata I	192.20	187.90	153.65	160.04	38.55	27.86	49.32	47.92	38.87	40.84	10.52	7.24	77-14	81-11	248-45	262-39
Toluca l. lineata II	194.59	191.82	156.44	162.61	38.15	29.21	57.87	56.99	45.16	47.43	12.87	9.78	93-16	90-12	293-59	263-42
Toluca l. varians	187.62	213.62	149.90	179.36	37.72	34.26	65.67	62.84	51.19	52.76	14.61	10.34	96-18	102-16	335-67	331-50
Sonora m. linearis	211.01	209.41	167.43	171.42	43.58	37.99	59.14	54.10	11.80	11.36	13.03	9.91	115-22	126-22	328-70	307-55
Sonora o. occipitalis	283.03	263.31	230.72	220.38	52.31	42.92	40.23	49.82	32.45	40.70	8.07	9.47	126-22	168-27	330-62	312-52
Sonora o. annulata	274.10	271.81	221.00	225.86	51.10	45.95	56.23	62.32	44.82	51.27	11.80	11.36	131-23	130-23	368-76	382-63
Chilomeniscus s. stramineus	183.95	196.09	156.95	172.05	27.00	24.05	26.51	34.57	22.91	30.39	3.79	4.41	111-15	96-12	230-31	244-29
Thamnophis hammondii	373.79	388.85	282.26	299.90	91.52	88.94	155.17	193.75	117.13	151.27	38.35	42.78	156-38	145-35	729-176	989-219
Thamnophis o. ordinoides	345.04	345.21	257.37	267.62	87.68	77.60	71.73	99.34	52.15	76.36	19.84	23.50	184-43	158-36	527-134	603-141
Thamnophis o. biscutatus	445.39	425.13	328.18	322.21	117.21	102.92	194.67	211.24	145.31	162.34	49.89	49.32	208-58	205-50	797-210	922-207
Conopsis nasus	234.17	230.93	198.76	203.37	35.41	27.56	60.79	57.57	51.58	50.83	9.41	6.89	100-14	105-13	334-49	344-38
Hypsiglena ochrorhynchus	290.31	270.23	240.53	230.43	49.78	39.80	53.79	70.21	43.78	59.58	10.39	10.80	168-27	157-21	391-67	375-52
Trimorphodon vandenburghi	555.23	556.00	464.64	477.13	90.59	78.88	114.21	249.10	95.67	215.49	19.14	33.89	264-45	234-35	738-114	1054-137
Tantilla eiseni	277.94	211.53	209.39	166.87	68.56	44.67	60.69	74.83	44.77	56.13	16.04	18.91	130-28	142-25	375-92	373-82
Elapsoidea niger	369.47	398.62	341.40	373.24	28.07	25.38	66.83	73.69	61.11	67.64	5.93	6.22	264-19	281-16	471-38	569-39
Micrurus a. mayensis ...	644.64	595.25	548.07	527.69	96.57	67.56	95.42	108.29	80.11	95.84	15.74	12.80	443-64	478-55	743-108	777-87
Micrurus n. nigrocinctus	458.13	527.91	394.41	476.38	63.72	51.53	179.16	233.76	152.72	210.58	26.62	23.42	218-29	220-21	745-113	890-88
Micrurus n. divaricatus	442.76	541.04	377.61	484.75	65.16	56.29	217.82	238.76	182.58	213.75	35.40	25.16	196-26	236-23	935-150	970-101
Agkistrodon m. mokeson	541.31	498.20	464.76	430.40	76.54	67.80	188.64	158.51	165.79	139.47	23.59	19.57	201-40	180-32	915-110	785-95
Trimeresurus gramineus	525.21	410.13	422.92	342.44	102.29	67.69	92.07	123.50	71.90	103.29	20.34	20.28	310-55	247-40	660-132	608-102
Trimeresurus elegans	725.06	613.42	595.12	514.00	129.94	99.42	209.98	232.43	170.55	196.21	39.94	36.33	430-75	387-61	1160-215	1151-184
Bothrops insularis ..	685.37	718.22	583.17	626.30	102.20	91.93	91.15	129.44	78.03	113.75	13.80	16.51	440-63	380-48	850-124	1000-118
Atheris squamigera ...	468.32	504.08	390.86	431.64	77.46	72.44	81.49	93.99	65.78	79.57	16.44	14.82	318-48	320-45	595-103	660-100

* The figures following hyphens are tail lengths.

TABLE 8

Assumed Standard Body Lengths
For Computation of Proportionalities and Sexual Dimorphism

				Sex Reaching Largest Size	
	Juvenile	Median	Adults	M	F
Lichanura r. roseofusca........	300	500	700		*
Adelphicos q. sargii	100	155	220		*
Geophis brachycephala	100	190	280	*	
Geophis nasalis	100	155	220	*	
Diadophis a. similis...............	110	205	300		*
Diadophis p. arnyi I.............	110	180	250		*
Diadophis p. arnyi II...........	110	180	250		*
Boaedon l. lineatus I.............	220	420	620		*
Boaedon l. lineatus II...........	200	325	450		*
Masticophis f. piceus...........	250	675	1100		
Masticophis lateralis	250	550	850		
Salvadora g. virgultea...........	250	475	700	*	
Phyllorhynchus b. browni....	160	230	300	*	
Phyllorhynchus d. nubilus....	160	230	300	*	
Phyllorhynchus d. perkinsi I..	160	280	400	*	
Phyllorhynchus d. perkinsi II	160	280	400	*	
Arizona e. occidentalis I........	250	525	800		
Arizona e. occidentalis II......	250	525	800		
Pituophis c. annectens	330	715	1100	*	
Pituophis c. deserticola I........	330	715	1100	*	
Pituophis c. deserticola II......	330	715	1100	*	
Lampropeltis g. californiae....	250	625	1000		
Rhinocheilus l. lecontei I......	200	450	700	*	
Rhinocheilus l. lecontei II....	200	450	700	*	
Rhinocheilus l. clarus...........	200	450	700	*	
Toluca l. lineata I.................	70	135	200		
Toluca l. lineata II...............	80	150	220	*	
Toluca l. varians	90	170	250		
Sonora m. linearis	100	175	250		
Sonora o. occipitalis...............	110	185	260		
Sonora o. annulata	110	185	260		
Chilomeniscus s. stramineus..	100	150	200		*
Thamnophis hammondii	120	285	450		*
Thamnophis o. ordinoides......	110	205	300		*
Thamnophis o. biscutatus......	200	400	600		*
Conopsis nasus	100	200	300		
Hypsiglena ochrorhynchus	140	220	300	*	
Trimorphodon vandenburghi	220	410	600		*
Tantilla eiseni	100	175	250		

TABLE 8
(continued)

	Juvenile	Median	Adults	Sex Reaching Largest Size	
				M	F
Elapsoidea niger	240	340	440		*
Micrurus a. mayensis	200	400	600		*
Micrurus n. nigrocinctus	200	400	600		*
Micrurus n. divaricatus	200	400	600		*
Agkistrodon m. mokeson	200	400	600	*	
Trimeresurus gramineus	200	350	500		
Trimeresurus elegans	350	675	1000		
Bothrops insularis	300	500	700		*
Atheris squamigera	270	385	500		*

Adelphicos qradrivirgatus sargii (Fischer)

This is a fine series in the collection of the California Academy of Sciences, from Finca El Cipres, Volcan Zunil, Guatemala. As noted by Mr. J. R. Slevin,[9] all specimens were dug out of piles of debris in a single locality; this is, therefore, an ideal series from the standpoint of territorial homogeneity. The size distribution is good. The nomenclature is that of Dr. H. M. Smith.[10]

Geophis brachycephala (Cope)

A series of moderate size from Boquete, Panamá, in the collection of the California Academy.[11] Although territorially well concentrated, the series of both sexes are somewhat lacking in adolescents.

Geophis nasalis (Cope)

A beautiful series taken by J. R. Slevin in cafetal debris at Finca El Cipres, Volcan Zunil, Guatemala.[12] All ages are represented. The nomenclature is that of Smith.[13]

Diadophis amabilis similis Blanchard.

A series from cismontane San Diego County, California, mostly in my own collection. The age distribution is good.

Diadophis punctatus arnyi (Kennicott)

I. A series in my collection from southern Kansas and northern Oklahoma.

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[9] Proc. Cal. Acad. Sci., Ser. 4, Vol. 23, No. 26, p. 403, 1939.
[10] Proc. Rochester Acad. Sci., Vol. 8, p. 192, 1942.
[11] Proc. Cal. Acad. Sci., Ser. 4, Vol. 23, No. 32, p. 474, 1942.
[12] Proc. Cal. Acad. Sci., Ser. 4, Vol. 23, No. 26, p. 404, 1939.
[13] Smithsonian Misc. Coll., Vol. 99, No. 19, p. 4, 1941.

TABLE 9
Tail Ratios

Species or Subspecies	Ratio of Tail Length to Length Over-all at Mean Length M	F	Ratio of Tail Length to Length of Body at Mean Length M	F	Males Juv.	Median	Adult	Females Juv.	Median	Adult	Coefficient of Ontogenetical Divergence* Male	Female
Lichanura r. roseofusca	.140	.133	.163	.153	.142	.164	.173	.144	.153	.157	19.7	8.6
Adelphicos q. sargii	.147	.116	.172	.132	.159	.171	.177	.128	.131	.132	10.7	3.1
Geophis brachycephala	.184	.161	.225	.192	.203	.222	.237	.192	.192	.193	15.5	0.5
Geophis nasalis	.169	.136	.203	.158	.172	.193	.212	.148	.152	.160	20.8	7.8
Diadophis a. similis	.192	.167	.238	.200	.210	.235	.244	.180	.197	.202	15.0	11.5
Diadophis p. arnyi I	.191	.157	.236	.186	.240	.236	.235	.186	.186	.186	− 2.1	0.0
Diadophis p. arnyi II	.188	.154	.231	.182	.211	.231	.240	.175	.182	.185	12.9	5.6
Boaedon l. lineatus I	.168	.123	.202	.141	.180	.199	.206	.127	.137	.141	13.5	10.5
Boaedon l. lineatus II	.182	.139	.223	.162	.194	.219	.230	.152	.159	.162	17.0	6.4
Masticophis f. piceus	.264	.269	.358	.368	.351	.358	.361	.379	.368	.366	2.8	− 3.5
Masticophis lateralis	.304	.298	.437	.424	.409	.435	.443	.412	.423	.426	8.0	3.3
Salvadora g. virgultea	.234	.227	.305	.294	.300	.304	.306	.290	.294	.295	2.0	1.7
Phyllorhynchus b. browni	.134	.081	.155	.087	.137	.155	.161	.085	.087	.088	16.1	3.5
Phyllorhynchus d. nubilus	.137	.081	.159	.088	.127	.154	.168	.088	.088	.088	27.8	0.0
Phyllorhynchus d. perkinsi I	.143	.099	.167	.107	.129	.166	.180	.098	.106	.110	33.0	11.5
Phyllorhynchus d. perkinsi II	.148	.099	.174	.109	.130	.169	.185	.104	.110	.113	34.9	8.3
Arizona e. occidentalis I	.134	.123	.155	.140	.161	.156	.154	.128	.140	.143	− 4.4	11.1
Arizona e. occidentalis II	.139	.125	.162	.143	.156	.161	.163	.137	.145	.148	4.4	7.7
Pituophis c. annectens	.170	.156	.204	.184	.212	.204	.201	.191	.182	.179	− 5.3	− 6.5
Pituophis c. deserticola I	.137	.126	.159	.145	.175	.159	.154	.155	.145	.142	− 12.8	− 8.8
Pituophis c. deserticola II	.148	.135	.174	.156	.176	.174	.174	.143	.156	.160	− 1.1	11.2
Lampropeltis g. californiae	.137	.131	.159	.150	.168	.156	.154	.155	.149	.148	− 8.7	− 4.6
Rhinocheilus l. lecontei I	.141	.130	.164	.149	.176	.165	.162	.155	.149	.147	− 8.3	− 5.3
Rhinocheilus l. lecontei II	.142	.132	.165	.152	.173	.166	.164	.146	.152	.154	− 5.3	5.3
Rhinocheilus l. clarus	.143	.131	.167	.151	.162	.166	.167	.124	.148	.156	3.0	22.9
Toluca l. lineata I	.201	.148	.251	.174	.230	.248	.255	.176	.174	.174	10.3	− 1.1
Toluca l. lineata II	.196	.152	.244	.180	.209	.242	.254	.158	.178	.185	19.4	15.7
Toluca l. varians	.201	.160	.252	.191	.231	.255	.264	.192	.191	.191	13.3	− 0.5
Sonora m. linearis	.207	.181	.260	.222	.248	.261	.267	.222	.222	.221	7.4	− 0.5
Sonora o. occipitalis	.185	.163	.227	.195	.215	.224	.228	.167	.190	.199	5.8	17.5
Sonora o. annulata	.194	.169	.204	.203	.228	.238	.242	.192	.201	.205	6.0	6.6
Chilomeniscus s. stramineus	.147	.123	.172	.140	.181	.173	.169	.142	.140	.139	− 6.9	− 2.1
Thamnophis hammondii	.249	.229	.324	.297	.325	.324	.324	.321	.297	.291	− 0.3	− 9.8
Thamnophis o. ordinoides	.254	.225	.341	.290	.288	.332	.345	.277	.287	.291	18.1	4.9
Thamnophis o. biscutatus	.263	.242	.357	.319	.369	.354	.349	.331	.316	.311	− 5.6	− 6.2
Conopsis nasus	.151	.119	.177	.136	.179	.178	.178	.139	.136	.134	− 0.6	− 3.7
Hypsiglena ochrorhynchus	.171	.147	.207	.173	.193	.205	.211	.169	.172	.174	8.9	2.9
Trimorphodon vandenburghi	.163	.142	.195	.165	.198	.195	.194	.176	.167	.163	− 2.1	− 7.7
Tantilla eiseni	.247	.211	.327	.268	.297	.322	.332	.225	.271	.289	11.1	24.9
Elapsoidea niger	.077	.064	.082	.068	.078	.082	.085	.056	.066	.071	8.6	23.6
Micrurus a. mayensis	.150	.114	.176	.128	.152	.171	.177	.126	.128	.128	15.2	1.6
Micrurus n. nigrocinctus	.139	.098	.162	.108	.150	.162	.165	.106	.108	.109	9.5	2.8
Micrurus n. divaricatus	.147	.104	.173	.116	.155	.174	.180	.115	.116	.116	14.9	0.9
Agkistrodon m. mokeson	.141	.136	.165	.158	.201	.169	.159	.182	.159	.151	− 23.3	− 18.6
Trimeresurus gramineus	.195	.165	.242	.198	.200	.234	.248	.199	.198	.197	21.4	− 1.0
Trimeresurus elegans	.179	.162	.218	.193	.210	.220	.223	.198	.191	.189	6.0	− 4.6
Bothrops insularis	.149	.128	.175	.147	.183	.177	.174	.158	.149	.146	− 5.0	− 7.9
Atheris squamigera	.165	.144	.198	.168	.181	.198	.206	.160	.166	.170	12.9	6.1

* A positive figure indicates a higher tail-length ratio in the adults than the juveniles.

II.   A second series from Tulsa, Oklahoma, and surrounding counties, the measurements having been made by the late Dr. Frank N. Blanchard, and sent me through the courtesy of Dr. H. K. Gloyd. I have kept the two series separate for comparative purposes. A few aberrant specimens were omitted in making the computations on Series II.

Boaedon lineatus lineatus Duméril & Bibron.

I.   A small series from Sipi and Butandiga, Uganda; and Kaimosi, Kenya Colony, Africa.

II.   A small series from Lamu Island, in the Coast Province of Kenya. While these series are rather inadequate in numbers, they are included to illustrate territorial differences within a subspecies. The measurements upon which the calculations are based were received through the courtesy of Mr. Arthur Loveridge.

Masticophis flagellum piceus (Cope)

A small but ontogenetically well-distributed series from San Diego County. Although a common snake, comparatively few of this species have complete tails, and even some of those which have been included in this study are not certainly complete.

Masticophis lateralis (Hallowell)

A small series from western San Diego County. Individuals of this species with complete tails are relatively rare, although the snakes themselves are quite common in this territory.

Salvadora grahamiae virgultea Bogert.

A small series from western San Diego County.

Phyllorhynchus browni browni Stejneger.

All available specimens were included; most of them are from the immediate vicinity of Tucson, Arizona. While inadequate in numbers (particularly the females) the data have been included for comparison with *decurtatus*. A single male juvenile has been triplicated.

Phyllorhynchus decurtatus nubilus Klauber.

A quite inadequate series from the vicinity of Tucson, included for purposes of comparison with the previous subspecies.

Phyllorhynchus decurtatus perkinsi Klauber.

I.   A large series, mostly in my own collection, from desert San Diego County.

II.   A small series from desert Riverside County, California, included for comparative purposes.

Arizona elegans occidentalis Blanchard.

I. A series from desert San Diego County; there being few juvenile males, the two smallest were duplicated.

II. A series from the Mohave-Victorville area of the Mohave Desert. The females are quite inadequate in number.

Pituophis catenifer annectens (Baird and Girard)

A large series restricted to western San Diego County. The juveniles are better represented than the adults; among the latter the dispersion is quite high.

Pituophis catenifer deserticola Stejneger.

I. A small series from Imperial County, California. One large aberrant female has been omitted.

II. A small series from the Mohave-Victorville section of the Mohave Desert. One aberrant male has been omitted.

Lampropeltis getulus californiae (Blainville)

A large series from San Diego County, including many juveniles born in captivity. All pattern phases have been included. This species shows high dispersion among the adults.

Rhinocheilus lecontei lecontei Baird and Girard.

I. A series from coastal San Diego County.

II. A series from the Mohave-Victorville section of the Mohave Desert. The female representation is inadequate.

Rhinocheilus lecontei clarus Klauber.

A series from eastern San Diego County; only 13 females are available.

Toluca lineata lineata Kennicott.

I. A series from the vicinity of Guerrero, Hidalgo, Mexico, the measurements of which were received through the courtesy of Dr. Hobart M. Smith. An aberrant male was excluded.

II. A second series, also from Dr. Smith, collected near Tezuitlan, Puebla, and adjacent Veracruz.

Toluca lineata varians (Bocourt)

A large, well-distributed series from Acultzingo, Veracruz, Mexico; the measurements are from Dr. Smith.

Sonora miniata linearis Stickel.

A good series from an island in Colorado River at Laguna Dam, close to the Imperial County, California, shore. This tiny island is only a few

hundred feet long and this series is therefore the most concentrated, territorially, of any available. Most of the specimens were collected by Wallace F. Wood and Joseph R. Slevin, and are in the CAS collection. The others are in the MVZ and LMK collections. Both sexes are well distributed ontogenetically.

Sonora occipitalis occipitalis (Hallowell)

A small series from the Mohave-Victorville area of the Mohave Desert. The females are few in number, and the juveniles of both sexes inadequately represented.

Sonora occipitalis annulata (Baird)

A good series from eastern San Diego and Imperial counties in California.

Chilomeniscus stramineus stramineus Cope.

A series reported on by Dr. J. M. Linsdale, from Eureka, in the Cape region of Lower California.[14] Re-measurements entailed some minor changes and the elimination of several specimens because of incomplete tails.

Thamnophis hammondii (Kennicott)

A large and ontogenetically well-distributed series from San Diego County.

Thamnophis ordinoides ordinoides (Baird and Girard)

A series from western Oregon, mostly from the vicinity of Portland. Ontogenetically, the distribution is good, although large adults are not plentiful.

Thamnophis ordinoides biscutatus (Cope)

A large series from the vicinity of Klamath Falls, Oregon, contained in the collections of the California Academy of Sciences and the Museum of Vertebrate Zoology. The measurements were given me by Dr. Henry S. Fitch.

Conopsis nasus Günther.

A good series in the Museum of Comparative Zoology, the measurements having been received through the courtesy of Drs. Edward H. Taylor and Hobart M. Smith. The specimens were collected at Alvarez, San Luis Potosí, Mexico. As both sexes are weak in juveniles, the available specimens have been duplicated.

Hypsiglena ochrorhynchus Cope.

A fair series from San Diego County. Specimens from both sides of the mountains are included, as no differences in tail proportionality are apparent.

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[14] Copeia 1936, p. 232.

Trimorphodon vandenburghi Klauber.

A small series from both sides of the mountains in San Diego County.

Tantilla eiseni Stejneger.

A small series from the coastal side of the mountains in San Diego County. Desert specimens had to be omitted, as they have proportionally shorter tails.

Elapsoidea niger Günther.

A series from Nyange, Amani, and Bumbuli, Tanganyika, Africa. The measurements were kindly furnished me by Mr. Arthur Loveridge.

Micrurus affinis mayensis Schmidt.

A small but ontogenetically well-distributed series from Yucatan, Mexico. The measurements of this, and the two following series of the same genus, were received through the courtesy of Mr. Karl P. Schmidt.

Micrurus nigrocinctus nigrocinctus (Girard)

A series from Panamá and the Canal Zone. One aberrant female has been omitted. The specimens are well distributed ontogenetically, but may not be territorially consistent.

Micrurus nigrocinctus divaricatus (Hallowell)

A well-balanced series from Honduras.

Agkistrodon mokeson mokeson (Daudin)

A large series from eastern Kansas, the measurements of which were received through the courtesy of Dr. Howard K. Gloyd. Several aberrant specimens have been omitted. The ontogenetic distribution is good; the dispersion is relatively high.

Trimeresurus gramineus (Shaw)

A small series from Formosa contained in the collection of the California Academy of Sciences.

Trimeresurus elegans (Gray)

A series from Ishigaki shima, Loo Choo Islands, Japan, also in the California Academy of Sciences collection.

Bothrops insularis (Amaral)

A series taken from data published by do Amaral.[15] Some obviously aberrant specimens were omitted; and, as there is a lack of juvenile males, 5 have been duplicated. All are from Queimada Grande Island, off the

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[15] Mem. Inst. Butantan, Vol. 1, No. 1, p. 62, 1921.

coast of Sao Paulo, Brazil, this being the only place where these snakes occur. Thus the series is territorially homogeneous.

Atheris squamigera (Hallowell)

A small series from Kaimosi, Nyanza Province, Kenya Colony, the measurements of which were courteously sent me by Mr. Arthur Loveridge. Owing to the lack of juvenile males, two were duplicated. One aberrant adult male was omitted.

I return now to the three questions which are among the primary purposes of this investigation. With regard to the first, that is, the linearity of regression, it is to be regretted that publication limitations allow the inclusion of only one of the scatter diagrams which have been prepared for each of the forms investigated (Fig. 1). All show substantially straight-line relationships, as is verified by the uniformly high values of the coefficients of correlation shown in Tables 5 and 6. In two or three series there seems to be evidence of an upward bending in the regression line of the males and a possible drooping in the females; but in any case this is so slight as to be below the level of significance in a linearity test. In a few forms there are indications of a slight droop in the regression line of the males, when the largest specimens are reached, as if the tail did not quite keep pace with the continued, but slow, growth of the body. But it can be fairly said, with respect to all of the species investigated, that, from a practical standpoint, the relationship between the length of tail and length over-all (or tail and body) is linear and may be treated as such in all difference computations. It is probably significant to observe that the greater the number of specimens in a series, the less any tendency to curvature is apparent.

I do not say that it is impossible to secure rather good fits with equations of the type $T = cL^k$, which have been shown by Huxley and others to be well suited to many problems of relative growth; rather, it is a fact that straight-line equations of the form $T = a + bL$ fit so well, and are so much easier to use in problems of taxonomic differences or sexual dimorphism, that I think they are to be preferred in practice, where their use is not inconsistent with the actual dispersions. I shall, however, in a later table, present some data on the constants c and k in the parabolic growth curves of several typical species.

As to the second question: Does the ratio of the tail length to total length remain constant, or vary with age? The answers are to be found in the values of a or a' (particularly the latter) in Tables 5 and 6. For, if the proportion does remain constant, then a and a' should equal zero. But we find that a and a' have relatively high values in many series; and, comparing these values with their standard errors—admittedly not a highly accurate procedure in this situation—half of them are found to be significant (the ratio being greater than 1.96) or highly significant

(ratio greater than 2.58). We have the following summary of the results derived from Table 6.[16]

Character of a'	Males	Females
Positive but not significant.....................	9	12
Positive and significant	..	2
Positive and highly significant	4	4
Sub-total	13	18
Negative but not significant.................	9	18
Negative and significant	8	5
Negative and highly significant..............	18	7
Sub-total	35	30
Grand total	48	48

We see, first, that more than half the males (30) have a value of a' differing significantly from zero, and more than one-third the females (18), as well. More than two-thirds of the males and nearly two-thirds of the females have negative values of a'. These proportions are too high to be due to chance. I think we may conclude that many species of snakes do change their tail proportionalities as they grow; that, of these, a majority have relatively longer tails as they age (a' negative), although a few have tails which become shorter, *Pituophis* and *Lampropeltis* being examples. In snakes in which the tails grow relatively faster than the bodies, the males are likely to exceed the females in disproportionate growth. This will be discussed further in connection with sexual dimorphism. Altogether, admitting that small and insignificant values of a' have little importance, and may result from the chance composition of the samples, we still find a considerable number of subspecies in which the change of tail-length proportionality with age is beyond question. Others, although failing in the test for mathematical significance, suggest, by the evidence of the graphical set-ups, that additional specimens would not be likely to reduce a' to zero.

There is found to be no correlation between the value of a' and adult tail-proportionality, using the appropriate figures in Tables 6 and 8 as criteria; rather, the change in proportionality—its direction and degree—seems to be a generic and even a species character without any widely applicable uniform rule of variation.

Species with negative constants which are outstandingly high are *L. r. roseofusca, G. nasalis, D. a. similis, B. l. lineatus, Phyllorhynchus*

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[16] To avoid the effects of spurious correlation, I have placed more emphasis on the T to B relationship in Table 6, than the more customary T to L relationship of Table 5.

(especially the males), *T. eiseni, T. gramineus* males, and *A. squamigera.* Those with high positive values are *Pituophis, L. g. californiae, A. m. mokeson,* and *B. insularis.* These latter are all short-tailed snakes, yet a decrease in tail proportionality with growth is not a universal characteristic of short-tailed snakes, as is shown by the presence of *Lichanura* and *Phyllorhynchus* in the other category.

The standard errors of b and b' given in Tables 5 and 6 are not set forth to indicate the significances of these statistics, since no such proof is required; a lack of significance would be equivalent to saying that the tail lengths of snakes are independent of body size, an obvious fallacy. But these standard errors are useful in giving a rough indication of the extent to which the population values of b and b' may differ from the values calculated from the available series. Confidence limits of the coefficients of correlation are omitted as having little interest in the present study.

The standard errors of estimate supply information on the extent of the dispersion of the specimens (in mm.) about the regression lines. The two final columns in Tables 5 and 6 present these figures reduced to percentages of the mean tail lengths; in this form they offer a more useful basis for comparison between species. The further use of this coefficient of variation, as an estimate of the dispersion at any age, will be referred to hereafter.

Table 7 gives the means and standard deviations of the measurements of the specimens upon which these studies have been based. The minimum and maximum limiting lengths listed in the final four columns are to be viewed in the light of the numbers of specimens available, as set forth in the first two columns in Tables 5 and 6. It is obvious that the larger the sample—if there has been no conscious selection of specimens—the closer will be the approach of the limiting specimens to true minima and maxima of the wild population. Practical conditions often prevent the collection of large specimens of the larger species, for which reason series of the smaller species of snakes are more likely to represent true field distributions. However, in some of the series treated it has been evident that the field men considered the juveniles too small to be worth-while.

In Table 8 I have indicated certain standard sizes at three ages, at which body proportionalities for comparative purposes are computed, as presented in Table 9. It is necessary to fix such standards if intersex and intersubspecific comparisons are to be made, since otherwise the averages M_B would not be the same for the groups compared. It will be noted that I have again used the body length rather than length over-all as the basic criterion; it seems to me that this constitutes a more pertinent and fairer method. For example, if we are comparing the tail lengths of a male and female, and we use snakes of the same length over-all, we are unduly penalizing the male, since we are really taking a smaller snake to compare with a larger, if, as we should, we view the tail as an appendage, rather than a section of the body of the animal itself.

The juvenile and adult standard sizes in Table 8 are not extremes, but rather are presumed to be averages of the young at birth, and large, but not record-breaking, adults. Further, the standard adult size represents large adults of the smaller of the sexes (in cases where one attains a conspicuously greater length than the other), since it was desired to limit calculations to lengths actually reached by both sexes, and thus avoid fictitious extrapolations. I have indicated in the same table by asterisks the cases in which one sex reaches a size notably larger than the other. The median length is not a true median derived from the sample, but is merely a half-way point between the other two terminal standards.

Table 9 presents the tail-length ratios at the mean lengths of the samples (first 4 columns), and also the proportionalities, calculated from the regression lines, at the selected standard body lengths. I should call attention particularly to the changes in proportionalities from the juvenile to the adult stages shown in the two final columns.[17] This is a reiteration of the statement that these ontogenetic variations are of importance in many genera; and, if comparisons of tail ratios are to be made between species, limited age groups must be used, or analytical methods of compensation should be employed, for some of these ontogenetical differences exceed 20 per cent. It will be noted that, in considerably more than half the series, the change in the male proportionality exceeds the female.

Should any doubt remain, upon the part of herpetologists who do not favor analytical methods, concerning the reality of these ontogenetic changes in tail ratio, I may cite, as a conspicuous example, the tail-to-body ratios of ten juvenile and ten adult male *P. d. perkinsi* selected at random from among the San Diego County specimens in my collection:

	Juvenile	Adult
	.133	.168
	.138	.187
	.135	.172
	.131	.178
	.130	.185
	.142	.179
	.141	.174
	.139	.170
	.139	.182
	.135	.165
mean	.136	.176

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[17] This difference has been given in terms of what may be called the "coefficient of ontogenetic divergence": $(P_j - P_a) / \frac{1}{2}(P_j + P_a)$ where P_j and P_a are the juvenile and adult proportionalities.

It will be observed that the juvenile with the highest ratio (.142) is considerably below the adult with the lowest (.165). It will be seen how questionable is the usual procedure of employing average tail-length ratios, in discussing species differences, without taking into consideration this extensive ontogenetic variation; for such an average figure is not so much a species characteristic as it is the result of the ontogenetic composition of the particular sample at hand.

I should call attention to the fact that a and a' are expressed in millimeters and therefore the values of these constants are not comparable between species; that is, the value of a does not in itself constitute a measure of ontogenetic variability, since a particular value would be of more importance in a small species than a large. In some ways the expression of the regression equations in the forms showing directly the nature of the variability in the tail-length ratios

$$T/L = a/L + b \quad \text{and} \quad T/B = a'/B + b'$$

shows the ontogenetic change most clearly, since a/L and a'/B are independent of the unit of measurement.

As I review the equations derived for these 48 species, and consider the inadequacies of several of the series, there are some concerning which changes may be prophesied when more material shall have become available.

In *A. q. sargii* I should expect a slightly steeper slope in the females; that is, a' will be increased negatively, and b' will also be higher. In female *G. brachycephala* a' will, I think, eventually be found to approximate -2. In *D. a. arnyi*, Series I, both sexes will develop larger negative values of a'. In *M. f. piceus* the female value of a' will tend to decrease. When larger series of *Phyllorhynchus* are available, all will more closely approach the regression line of San Diego County *perkinsi*. In *A. e. occidentalis* males, Series I, with a more adequate series of juveniles, I should expect a' to become negative. In *P. c. deserticola* females, Series II, the high negative value of a' is probably accidental, and not truly representative. In *Conopsis nasus* a more adequate juvenile representation would probably increase the negative value of a' in the males.

In addition to the 48 series of which both analytic and graphic investigations were made, there are available 27 additional series which were not considered sufficiently extensive, or territorially compact, to justify an analytic study. However, a simple graphic determination of the regression lines of T on B has been made, with the results as set forth in Table 10. These may be compared with related species in Table 6. Again we note that negative values of a' predominate, particularly among the males.

In Table 11 statistics similarly derived are given for a number of subspecies of garter snakes. For the basic measurements of most of these I am greatly indebted to Dr. Henry S. Fitch. For comparative purposes the

TABLE 10

Relationship of Tail Length to Body Length—Supplementary Series

Species or Subspecies	Area	Number of Specimens		Regression Coefficient, b'		Regression Constant, a'		Standard Adult Body Length mm.	Ratio of Tail Length to Body Length at Standard Adult Body Length	
		M	F	M	F	M	F		M	F
Charina bottae	Entire range	47	50	.171	.133	−6.3	−0.9	450	.157	.131
Geophis semidoliatus	Cuautlapan, Veracruz	46	49	.136	.095	−1.4	0.8	220	.130	.099
Ninia psephota	Boquete, Panama	11	18	.439	.398	−14.4	−15.4	350	.398	.354
Ninia sebae morleyi	Chichen Itzá, Yucatan	10	16	.348	.218	−12.1	0.6	250	.300	.220
Dialophis amabilis modestus	Los Angeles Co., Calif.	11	14	.276	.235	−6.0	−2.2	300	.256	.228
Lycophidion capense ornatum	Uganda	20	27	.239	.202	−17.3	−18.0	350	.190	.151
Coluber constrictor constrictor	Southeast, N. C. to La.	46	44	.383	.353	−3.3	−3.0	900	.379	.350
Coluber constrictor flaviventris	Kansas	30	29	.342	.316	−2.1	−3.9	800	.339	.311
Coluber constrictor mormon	Entire range	66	97	.377	.348	−8.8	−5.1	750	.365	.341
Masticophis flagellum flagellum	Southeast, N. C. to La.	13	18	.346	.319	−8.1	10.5	1300	.340	.327
Masticophis flagellum testaceus	Entire range	21	27	.337	.319	2.9	0.9	1200	.339	.320
Masticophis flagellum piceus	Cape region, B. C.	16	19	.366	.359	−5.7	6.0	1100	.361	.365
Masticophis taeniatus taeniatus	Entire range	22	33	.492	.466	−47.8	−25.2	1000	.444	.441
Phyllorhynchus decurtatus perkinsi	Sw. Arizona	28	9	.217	.117	−12.0	−2.4	400	.187	.111
Elaphe rufodorsata	Soochow, China	34	39	.244	.193	−0.4	−1.2	500	.243	.191
Arizona elegans elegans	Kan., Okla., Texas	17	19	.172	.167	1.4	−0.4	900	.174	.167
Pituophis sayi affinis	Central Arizona	23	27	.151	.133	6.2	6.6	1200	.156	.139
Pituophis sayi affinis	Yuma Co., Arizona	16	15	.157	.136	2.3	6.3	1200	.159	.141
Lampropeltis multicincta	Entire range	44	53	.188	.171	−3.3	2.3	600	.182	.175
Rhinocheilus lecontei lecontei	Central Arizona	39	25	.171	.160	−0.1	−2.3	650	.171	.156
Rhinocheilus lecontei tessellatus	Texas	34	21	.175	.166	−0.1	−1.7	700	.175	.164
Sonora episcopa	Kansas, Oklahoma	21	22	.258	.209	0.0	0.7	220	.258	.212
Sonora miniata linearis	Entire range*	19	9	.282	.222	−4.5	0.2	300	.267	.223
Natrix tigrina tigrina	Yokohama, Japan	28	22	.326	.282	−7.7	−3.9	600	.313	.275
Coniophanes fissidens punctigularis	Volcan Zunil, Guatemala	26	15	.570	.428	−9.4	−3.1	250	.532	.416
Tantilla gracilis	Entire range	20	23	.378	.300	−8.0	−3.5	150	.325	.277
Trimeresurus albolabris	Nodoa, Hainan, China	21	19	.378	.205	−47.0	−11.4	500	.284	.182

* Except Laguna Island.

data on three series, *T. o. biscutatus, T. hammondii,* and *T. o. ordinoides* (vicinity of Portland), are carried forward from Tables 6 and 9. A considerable consistency in adult proportionalities will be found evident in the last two columns of Table 11, both between territorial groups of the same race, and between races. It is of interest to note these adult tail-length proportionalities in the light of the relationships deduced by Dr. Fitch in his monograph.[18]

On page 8 I have given an equation showing how the mean of the tail ratios $M_{T/L}$ (or $M_{T/B}$), which involves many individual computations, may be derived from the mean of the tails divided by the mean of the lengths over-all, or body lengths (M_T/M_L or M_T/M_B) from other statistics readily available, provided the coefficients of correlation have been calculated. In order to ascertain the importance of the differences between these statistics, I have made four example computations with the following results, which are given in terms of the multiplier to be applied to M_T/M_L in order to derive $M_{T/L}$:

| | Multiplier | |
Species	Male	Female
P. d. perkinsi (S. D. Co.)	0.9849	0.9926
S. o. annulata	0.9977	0.9969

It will be observed that in these four examples, where the samples are fairly large and the correlation high, the mean proportion differs from the proportion of the means by a maximum of 1.5 per cent. The latter proportion therefore may well serve as an approximation. It is to be remembered that neither of these statistics is particularly useful, since both depend too much on the ontogenetic distribution of the samples. Should a single statement of tail proportionality be desired to represent a species in making interspecific comparisons, and it is not possible to restrict the statement to some particular age (juvenile or adult, for example) then I should recommend the use of the proportion at the median length, as determined from the regression equation. But for most taxonomic studies adult proportionalities are to be preferred, as will be discussed hereafter.

With respect to the figures given in Tables 5 to 9, it should be stated that all of the derived statistics were calculated to a further degree of accuracy than shown, usually to 6 figures after the decimal point. This was done so that the derived statistics would not lose in accuracy through rounding off; however, these additional figures are not entered in the tables, as they would lead only to confusion and difficulty in making comparisons, and would give an entirely unwarranted impression with respect to the accuracy of the results. This matter of dropping figures is

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[18] A Biogeographical Study of the *Ordinoides* Artenkreis of Garter Snakes (Genus *Thamnophis*). Univ. Calif. Pubs. in Zoöl., Vol. 44, pp. 1-150, 1940.

TABLE 11

Relationship of Tail Length to Body Length—*Thamnophis*

Species or Subspecies	Area	Number of Specimens		Regression Coefficient, b′		Regression Constant, a′		Standard Adult Body Length mm.	Ratio of Tail Length to Body Length at Standard Adult Body Length	
		M	F	M	F	M	F		M	F
Thamnophis ordinoides vagrans	Nevada, Utah	66	73	.345	.298	−1.5	3.3	500	.342	.305
Thamnophis ordinoides biscutatus	Klamath region	107	95	.338	.300	6.1	6.1	600	.349	.311
Thamnophis ordinoides elegans	Lassen, Modoc, Shasta, Plumas Cos.	29	29	.393	.340	−11.5	−7.0	500	.370	.326
Thamnophis ordinoides hydrophila	Sw. Oregon	49	42	.402	.360	−9.8	−7.0	500	.382	.346
Thamnophis ordinoides hydrophila	Humboldt, Mendocino Cos.	56	58	.400	.354	−10.0	−6.9	400	.375	.337
Thamnophis ordinoides couchii	Cromberg, Plumas Co.	15	16	.362	.299	−6.8	−5.8	500	.326	.287
Thamnophis hammondii	San Diego County	168	153	.324	.280	0.1	4.9	450	.324	.291
Thamnophis hammondii	Northern Lower California	19	25	.344	.297	−6.7	0.6	450	.329	.298
Thamnophis digueti	Lower California	14	17	.340	.304	−8.5	−5.5	500	.323	.293
Thamnophis ordinoides atratus	Humboldt, Mendocino Cos.	51	58	.383	.329	−5.3	−1.9	400	.370	.324
Thamnophis ordinoides atratus	S. F. Bay region	61	65	.383	.325	−7.3	−0.5	450	.367	.324
Thamnophis ordinoides	Canada	8	20	.383	.305	−7.8	−4.0	350	.361	.294
Thamnophis ordinoides	Washington	18	38	.365	.300	−9.5	−3.0	350	.338	.291
Thamnophis ordinoides	Vicinity of Portland	74	84	.374	.299	−8.5	−2.4	300	.345	.291
Thamnophis ordinoides	Sw. Oregon, Nw. Calif.	66	104	.390	.325	−9.0	−5.0	350	.364	.291
Thamnophis marcianus	Arizona	16	24	.309	.266	1.0	6.3	500	.311	.253

mentioned only to explain seeming inaccuracies which may be found if an attempt be made to check some of the derived statistics.

Parabolic equations of the form $Y = cX^k$ are frequently found to fit quite closely the growth of body parts.[19] They are also to be preferred on certain theoretical bases. However, in the present study, as was the case with rattlesnake heads,[20] I do not find that the tail follows a curve of the form $T = cL^k$ any closer than a straight line of the form $T = a + bL$; in fact, in most cases the straight line gives the better fit. And the straight line is so much easier to use, in evaluating sexual dimorphism or species differences, that, if a fit is at all close, it is definitely to be preferred to the more complicated equation.[21] In the present instance the high values of the correlation coefficients (Tables 5 and 6) are in themselves a proof of the closeness of fit of the straight lines. The parabola seems to me to have only one recommendation in the present case; since the deviations from the regression line are measured logarithmically, the juveniles are given a proper weight as compared with the adults. In the present study, as the straight line is to be preferred both on the score of closeness of fit and simplicity, I shall go no further into the parabolas than to list in Table 12 the constants c and k in the equation $T = cL^k$ for those seventeen of the series previously discussed, which contain the most specimens. This will serve to illustrate the magnitude of these constants in example series.

As to the third problem, that is, the nature of the dispersion of the individual specimens about the regression line, here again we are somewhat dependent upon the graphic studies which cannot be presented. As was the case with head-length studies in the rattlesnakes,[22] it is clear that the dispersion is substantially proportional to the tail length. Thus the scatter widens toward the larger sizes, the points representing the individual specimens filling an angular space about the regression line (Fig 1). On the assumption that the dispersion is proportionate to tail length, the coefficient of variation would remain constant from the juvenile to the adult state, instead of there being constancy in the standard deviation

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[19] Julian Huxley: Problems of Relative Growth, New York, 1932, p. 4; D'Arcy Wentworth Thompson: On Growth and Form, Cambridge, 1942, p. 205.

[20] Occ. Papers S. D. Soc. Nat. Hist., No. 4, p. 7, 1938.

[21] Of course, the two curves give the same line if $a = 0$, for then $k = 1$, and $b = c$. Therefore, it would be expected that the parabolic expression would give a good fit where a is small, even though the relationship be truly linear. I have mentioned the fact that in one or two cases some evidence of an upward curve is present, while a few others seem to droop, especially when the larger specimens are reached. These curves indicate that the equation $T = cL^k$ might be appropriate, an upward curve indicating a value of k greater than unity, while in a dropping curve k is less than one.

[22] Occ. Papers, S. D. Soc. Nat. Hist., No. 4, pp. 11-17, 1938. As other references to this rattlesnake head-length study are made hereafter, to avoid confusion I should call attention to the fact that in the former paper I used a as the regression coefficient and b as the regression constant $(H = aL + b)$; while in the present paper, following a more general custom, I have reversed the symbolism $(T = a + bL)$.

TABLE 12

Constants of Tail-length Equations of the Form $T = cL^k$

Species	Males		Females	
	k	c	k	c
Lichanura r. roseofusca	1.221	.0344	1.071	.0851
Adelphicos q. sargii	1.113	.0802	1.132	.0582
Geophis nasalis	1.179	.0635	1.123	.0692
Diadophis a. similis	1.149	.0845	1.059	.1205
Diadophis p. arnyi II	1.213	.0594	1.058	.1125
Phyllorhynchus d. perkinsi I	1.227	.0383	1.147	.0417
Pituophis c. annectens	1.000	.1710	0.965	.1963
Lampropeltis g. californiae	0.954	.1866	1.007	.1211
Toluca l. varians	1.176	.0800	1.096	.0964
Sonora m. linearis	1.127	.1047	1.007	.1734
Sonora o. annulata	1.101	.1130	1.045	.1334
Thamnophis hammondii	1.003	.2415	0.933	.3404
Thamnophis o. ordinoides	1.068	.1718	1.048	.1722
Thamnophis o. biscutatus	1.003	.2564	0.969	.2904
Conopsis nasus	1.056	.1119	1.014	.1125
Agkistrodon m. mokeson	0.839	.3926	0.859	.3311
Bothrops insularis	1.006	.1429	1.003	.1253

about the regression line (the standard error of estimate), as is the case in most correlation problems. This is equivalent to saying that, in these snakes, any deviation in the tail length of an individual from the mean at his age is maintained through life without change in proportionality; in other words, a snake which starts life with a tail 10 per cent longer than average will continue to have a tail 10 per cent longer as it grows. The following statistics of a few restricted-length groups of juveniles and adults will show that this relationship is substantially true.[23] The groups selected are from among those treated in Tables 5 to 9.

Comparative Standard Errors of Estimate

Species	Males		Females	
	Juvenile	Adult	Juvenile	Adult
Phyllorhynchus d. perkinsi, I	5.77	4.63	6.06	5.88
Pituophis c. annectens	6.89	7.12	6.66	5.58
Sonora m. linearis	1.64	1.93	1.85	1.88

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[23] *Loc. cit.* pp. 11-17. See the more elaborate discussion of this relationship in the head lengths of rattlesnakes, wherein the same approximate constancy in the coefficient of variation was found.

In half these cases the adult variation is lower than the juvenile; in half the contrary is true. This substantiates the results derived in the studies of rattlesnake head dimensions (*loc. cit.* p. 17), where much larger series were available. I think, based on such figures, and the graphical studies of every species, that we may assume a constant percentage deviation about the regression line. This will greatly expedite studies of species differences and sexual dimorphism, as will be subsequently discussed.

Correlation of Tail Length and Body Thickness

The fact that slim snakes have long tails, and stout snakes short, is evident from observation. An endeavor was made to reduce the relationship to figures. The results are rather inadequate, because of the difficulty of measuring body diameters accurately, particularly after preservation. Although the expected relationship is found to exist, the correlation is not especially close.

From 8 to 20 specimens of each of 15 species of snakes were measured at mid-body. The average values of the body width, or thickness, as a percentage of body length, (a quantity which might well be called the index of attenuation of a snake) were ascertained. These figures were correlated with the tail-to-body ratios, also expressed as percentages. In determining a representative figure for the latter, the proportions at median body length were used, the sexes being averaged. The resulting data follow:

RATIOS IN PER CENT

Series	W/B	T/B
L. r. roseofusca	3.04	15.8
A. q. sargii	2.90	15.1
G. brachycephala	3.22	20.7
G. nasalis	3.55	17.2
D. a. similis	2.22	21.6
M. f. piceus	1.89	36.3
M. lateralis	1.78	42.9
P. d. perkinsi	2.72	13.6
A. e. occidentalis	2.24	14.8
P. c. annectens	2.45	19.3
R. l. lecontei	2.44	15.7
S. m. linearis	2.36	24.1
S. o. annulata	2.69	21.9
T. vandenburghi	2.02	18.1
T. eiseni	2.19	29.6

The correlation between these pairs of figures was calculated and found to be -0.558. This is significant ($P = 0.029$). The regression equation is $Y = 3.3 - 0.036 X$, where X is the tail-to-body ratio and Y is the width-

to-body ratio, both figures being expressed as percentages. The adherence of the several species to the regression line is not particularly close.

T. vandenburghi has a short tail for so slim a snake; while the two *Geophis* have overly long tails for their relatively stout bodies. The parabola $Y = 5.68 - 0.199\,X + 0.00258\,X^2$ fits the points somewhat better than the straight line, but the deviations of some of the species remain considerable.

DIFFERENCE PROBLEMS

Having developed certain generalities with respect to the nature of the variation of tail lengths in snakes, it becomes desirable to show how these affect the calculations in difference problems. For the methods thus far developed only have value if it can be shown that their use will facilitate and render more accurate the evaluation of differences. As compared to problems involving differences in lepidosis, the characters of which are presumed to remain unchanged throughout life, we have here the complication of a character subject to ontogenetic change, both in proportionality and dispersion.

It is possible, by the method of the analysis of covariance, to determine the significance of the difference between the values from which two regression lines have been evolved. In the present case, however, I do not think we are interested in the average, or over-all, differences throughout life; rather, we are usually concerned with the difference at some particular time of life, often the adult stage,[24] or at some particular body size. If we are to deal with tail-length directly, rather than with proportionality, we must have some method whereby the data of all specimens can be transformed to usefulness at the size at which the computation is to be made. This can be easily done if we assume linearity of regression and constancy of the coefficient of variation, both of which suppositions have been found substantially true in all the species investigated. One method is to determine a probable tail length for each specimen at some assumed standard body length, and thus have available an array of tail lengths which represent a hypothetical assemblage of snakes of that standard and uniform body size. However, this rather laborious process, involving a separate calculation for each specimen, which was used in the investigation of rattlesnake head problems (*loc. cit.* p. 22), can be much simplified, and the same result attained, by a modified method. We first determine the standard error of estimate of T on L (or B). This is taken as the standard deviation of the tail lengths of snakes at length M_L (or M_B). Dividing this standard error by the mean tail length M_T gives the coefficient of variation, which is presumed to remain constant at all ages. From this, in turn, the standard deviation of the tail lengths at any assumed body length may be readily computed. For example, let it be desired to determine

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[24] See diagram *loc. cit.*, p. 21.

the probable dispersion in the tail length of snakes of a certain species at any arbitrary body length B_1. We first derive from the entire sample the regression equation $T = a' + b'B$, the standard error of estimate $\sigma_{T.B}$, and the mean length of tail M_T. The value of V is found from $V = \sigma_{T.B}/M_T$. The mean tail length at body length B_1 is found from $T_1 = a' + b'B_1$, and the desired dispersion is found from $\sigma_{T_1} = VT_1 = \sigma_{T.B} (a' + b'B_1)/M_T$. Having done the same with the other species or group with which a comparison is desired, the two tail-length arrays can be compared by the method of determining the significance of the difference between two means, for we have available all the required statistics: the two means, the standard deviations of the arrays, and the number of specimens in each sample. Of course, the same standard body length B_1 must be used for both species. The full number of specimens in each sample may be used as N_1 and N_2,[25] as all specimens have entered into the derivation of the regression line and the dispersion about that line. Either of two methods of testing the significance of the difference between means may be employed.[26]

For example, we shall test the difference between the tail lengths in adult *Pituophis c. deserticola* as found in Imperial County and in the Mohave-Victorville area of California. It first becomes necessary to select a standard body length at which the difference will be calculated. This should usually be an adult length, since, as will be shown in studies of sexual dimorphism, differences in tail length tend to reach their maxima in the adult stage.

We take our standard lengths of *Pituophis* at a body length of 1100 mm. (Table 8.) Using the regression formulas already derived (Table 6), we find the following mean tail lengths of snakes of this size:

Area	Males	Females
Imperial County	169.01	155.70
Mohave-Victorville	190.90	176.39

The corresponding standard deviations of the tail length at this standard body length, as derived from the equations above given and using the values of V, the mean coefficient of variation, set forth in the two final columns of Table 6 are:

Area	Males	Females
Imperial County	8.89	7.67
Mohave-Victorville	11.08	8.99

Applying the null method for determining the significance of the difference between two means, we find that both sexes show highly sig-

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[25] This use of the full values N_1 and N_2, is a somewhat questionable procedure if the ontogenetic distribution of the sample is poor.

[26] Kenney, Part II, p. 140; Simpson and Roe, p. 192.

TABLE 13

Adult Tail-length Differences
(Expressed in Terms of the
Coefficient of Divergence in Per Cent)

	Males	Females
(*Geophis brachycephala* from Panamá and (*Geophis nasalis* from Guatemala	8.94**	18.09**
(*Diadophis a. similis* from San Diego and (*Diadophis p. arnyi* II from vic. of Tulsa	0.33	7.48**
(*Diadophis p. arnyi* I from S. Kansas and N. Oklahoma and (*Diadophis p. arnyi* II from vic. of Tulsa	− 2.33*	0.32
(*Boaedon l. lineatus* I from Supi, Butandiga and Kaimosi and (*Boaedon l. lineatus* II from Lamu Island	− 14.19**	− 15.78**
(*Phyllorhynchus b. browni* vic. Tucson and (*Phyllorhynchus d. nubilis* vic. Tucson	− 4.64	0.42
(*Phyllorhynchus d. perkinsi* I San Diego County and (*Phyllorhynchus d. perkinsi* II Riverside County	− 2.72	− 2.47
(*Arizona e. occidentalis* I San Diego County ond (*Arizona e. occidentalis* II Mohave Desert	− 5.74**	− 2.76*
(*Pituophis c. annectens* San Diego County and (*Pituophis c. deserticola* I Imperial County	26.86**	23.28**
(*Pituophis c. deserticola* II Mohave Desert and (*Pituophis c. deserticola* I Imperial County	12.16**	12.45**
(*Rhinocheilus l. lecontei* I San Diego County and (*Rhinocheilus l. lecontei* II Mohave Desert	− 1.40	− 4.70*
(*Rhinocheilus l. lecontei* I San Diego County and (*Rhinocheilus l. clarus* San Diego County	− 3.16*	− 5.70**
(*Toluca l. lineata* I Hidalgo and (*Toluca l. lineata* II Puebla & Veracruz	1.42	− 5.62**
(*Toluca l. lineata* II Puebla & Veracruz and (*Toluca l. varians* Veracruz	− 2.61*	− 3.02
(*Sonora o. occipitalis* Mohave Desert and (*Sonora o. annulata* San Diego and Imperial counties	− 6.04**	− 2.93
(*Thamnophis o. ordinoides* vic. Portland and (*Thamnophis o. biscutatus* vic. Klamath Falls	− 3.72**	− 9.66**
(*Micrurus n. nigrocinctus* vic. Panamá and (*Micrurus n. divaricatus* Honduras	− 8.55**	− 6.88**

* Significant (*P* below 5 per cent); ** highly significant (*P* below one per cent). If the value given is positive, the first named form has the longer tail; if negative, the second is the longer-tailed.

nificant territorial differences; that is, the Mohave-Victorville snakes are definitely longer-tailed than those from Imperial County, the differences not being attributable to the chance composition of the samples. The racial dimorphism, or divergence, measured in terms of the coefficient of divergence, is 12.16 per cent, in the males, and 12.45 per cent in the females.

Using the same method, all the pairs listed in Table 13 were investigated, taking the pertinent statistics from Tables 5 to 9. The results are given in terms of the adult coefficient of racial divergence, those showing significant differences (*P* less than 5 per cent) being starred, while those which are highly significant (*P* less than one per cent) are double starred.

In six of these pairs the standard adult sizes of the two components differ somewhat (third column of Table 8); these are *G. brachycephala-nasalis*, *D. a. similis–p. arnyi* II, *B. l. lineatus* I–*lineatus* II, *T. l. lineata* I–*lineata* II, *T. l. lineata* II–*varians*, and *T. o. ordinoides–biscutatus*. In two cases, *Boaedon* and *Thamnophis*, the differences are relatively great. The question naturally arises whether the method of evaluating differences which I have used is a proper one in such situations, for by this method one really compares the tail proportionality of an adolescent or young adult of the larger form with a true adult of the smaller. This somewhat involved problem has been discussed before, in the investigation of the head sizes of rattlesnakes.[27] In tail length investigations I should recommend that, if the standard adult body length of the larger form exceeds the smaller by more than 50 per cent, then a modified method should be employed as follows: Make the comparisons at the standard adult length of the smaller form as before, but instead of calculating the tail length of the larger from its regression line, calculate it from its own proportion at standard adult body length. For example, take the comparison between male *T. o. ordinoides* from the vicinity of Portland and *T. o. biscutatus* from the vicinity of Klamath Falls. The standard adult length of the former is taken at 300 mm. and of the latter, a much larger snake, at 600 mm. We find that *ordinoides* at 300 mm. has a tail length averaging 103.61 mm., while *biscutatus* at the same length has an average tail length of 107.54 mm. This difference is found to be significant; however, as above mentioned, we have really compared an adult *ordinoides* with an adolescent *biscutatus*. Now, *biscutatus* at its adult length of 600 mm. has a tail ratio of 0.349. Therefore, at 300 mm. a hypothetical adult *biscutatus* would have a tail length of 104.70 mm. The difference, formerly 3.93 mm., is now reduced to 1.09 mm. and this is not significant. A similar treatment of the *Boaedon* problem and female *Thamnophis*, however, does not change the former conclusions; all differences remain significant. This is a somewhat modified method of making a correction for differences in ultimate length from that utilized in the head-length

[27] Occ. Papers, S. D. Soc. Nat. Hist., No. 4, p. 34. The problem is of particular interest in comparing the body proportions of stunted races with the parent forms from which they were derived (see p. 29).

study.[28] It may be pointed out that if our object is solely the demonstration of specific or subspecific differences, the mere fact that these special provisions for taking care of differences in ultimate length are necessary, are, in themselves, evidence of interspecific or subspecific differences.

The results of these example difference investigations represent too many entirely unconnected taxonomic problems to warrant discussion; it could not be expected that they would suggest any general relationships. They are, after all, offered only to illustrate a method of test; to show how similar, but more unified, problems might be handled in a monographic treatment of a genus. It will be observed that two species (or subspecies) may differ significantly in the tail proportionality of one sex, while none is evident in the other. One surprising result is the high difference between *Pituophis c. annectens* and *P. c. deserticola*, and the somewhat reduced, but still considerable difference, between the desert gopher snakes of Imperial County and those of the Mohave Desert. This should naturally suggest a further investigation of these two populations, now usually considered to belong to a single subspecies, *deserticola*.

I have mentioned before how necessary it is, if an investigation of tail length is to be thorough, that the specimens be plotted so that the aberrants may be carefully resurveyed. By this means many cases of inaccurate measurements, incorrect sexing, incomplete tails, misidentifications, and other mistakes (besides true aberrants) will be disclosed. Such was the case in the series used in the present investigation, for a number of errors of all these classes were found and corrected; had they not been discovered they would have affected the calculated proportionalities considerably.

Following this method through, it is feasible, if the analytical data be available, to determine the probability that a particular specimen belongs in a specific category. For example, let us consider the *Lampropeltis zonata-multicincta* problem.[29] For the purposes of this example I am going to assume a territorial homogeneity in the tail length of this species which may or may not be justified; we do not know the type locality of Blainville's doubtful specimen and therefore I shall use all available mountain king snakes for comparison. Blainville mentions particularly the sharp tail of his specimen, from which it may be assumed that the tail was complete.

From a study of 44 males and 53 females, we find that the tail length equation of the males is $T = -3.3 + 0.188B$, and of the females $T = 2.3 + 0.171B$. Blainville's specimen had a body length of 360 mm. (Burt's translation). At this body length the average male would have a tail length of 64.38 mm., while the average female would have a

[28] *Loc. cit.*, p. 34.

[29] Charles E. Burt: The Nomenclature of Western Coral King Snakes, *Lampropeltis zonata* Versus *L. multicincta*, Copeia No. 2 of 1936, p. 94. For a history of the case see the bibliography in Burt's paper together with James L. Peters, Copeia, No. 2 of 1938, p. 93.

tail length of 63.86 mm. Our analysis of the original data produces the following values of V: males, 7.86 per cent; females, 10.19 per cent. From these figures we deduce the following standard deviations in the tails of specimens having the average tail lengths given above: males, 5.06 mm.; females, 6.51 mm. Blainville's specimen had a tail length of 55 mm.; thus differing from the average male snake of this body size by 9.38 mm., and from the average female by 8.86 mm. Dividing these values by the respective standard deviations, we have these resultant values of t: males, 1.85; females, 1.36. From a t-table we find that about 7.2 per cent of males, and 18.1 per cent of females would show as great a deviation from the respective means as does this specimen; half of these would be this much smaller than average, the other half larger. Thus about 3.6 per cent of male snakes and 9 per cent of females of this species would be expected to have a tail as short as Blainville's specimen. Our conclusion is that, while Blainville's type had a rather short tail for a California coral king snake, it is by no means impossible that it may have represented that species, as far as the tail-length criterion is concerned. If it was a coral king snake, the odds favor its having been a female.

It may prove interesting to investigate the other species to which Blainville's type specimen might have belonged, using the criteria of pattern, length over-all, and tail proportionality. The ringed or half-ringed snakes of the area from which Blainville's other types came are the following:

Lampropeltis getulus californiae (ringed phase)
Lampropeltis multicincta
Rhinocheilus lecontei lecontei
Rhinocheilus lecontei clarus
Sonora occipitalis occipitalis
Sonora occipitalis annulata
Sonora semiannulata semiannulata
Chilomeniscus cinctus

The last two are quite ruled out by considerations of size, as indeed are the other two Sonoras as well, yet I shall apply the tail-length test to the latter. Proceeding with the method previously illustrated in the case of the coral king snake, *multicincta*, and repeating the figures derived for that species, we have the following values of the proportion of specimens of each species that would show as great a difference from the average as does Blainville's type, and in the same direction:

	Proportion, Per Cent	
	Male	Female
L. g. californiae	32.0	47.0
L. multicincta	3.6	9.0
R. l. lecontei	5.5	3.6
R. l. clarus	5.2	12.5
S. o. occipitalis	0.01−	0.02
S. o. annulata	0.01−	0.01

It is evident that the Sonoras do not fit; not only are they too small, but their tails are proportionately much longer than the Blainville type. The two subspecies of *Rhinocheilus* are possibilities, but do not fit the pattern description, since the rings of *Rhinocheilus* are not complete ventrally. As far as tail length is concerned, Blainville's type is nearer *L. g. californiae* than *L. multicincta*; in fact, it fits unusually well. Male *L. g. californiae* with a body length of 360 mm. would have an average tail length of 58.38 mm., while females would average 54.58. These are very close to the 55 mm. of the Blainville type. But the pattern described by Blainville does not fit the ringed phase of *californiae*, particularly the 2 half rings on the head. Young specimens of *californiae* are very dark brown, but Blainville would hardly have referred to them as black. Thus the coral king snake remains the best possibility, although clearly the identification is quite uncertain. The tail-length survey surely throws additional doubt on the allocation of Blainville's snake to *L. multicincta;* and *zonata*, if it is to be considered valid, must be based on Lockington rather than Blainville. Hence the decision becomes one of the interpretation of the Code of Nomenclature, as discussed by Linsdale, Burt, and Peters.

In a problem of this character, if one can make a graphic determination of the regression lines, it would probably be satisfactory to assume V at 8 per cent, judging by the values of V found in the 48 species analytically investigated and set forth in the last two columns of Table 6. *Lampropeltis* seems to be a genus with rather higher values of V than most snakes.

SEXUAL DIMORPHISM

The coefficient of divergence, and the method, hitherto developed, of deriving hypothetical tail-length arrays at any standard body size, afford useful statistics for investigating and stating the extent and significance [30] of sexual dimorphism in tail length. The series listed in Tables 5 to 9 have therefore been surveyed, with the results set forth in Table 14. While

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[30] The term as here used does not connote a determination of the reasons for sexual dimorphism and its interspecific variations; here significance is used in its mathematical sense and refers to the determination whether any intersex difference found might result from the chance composition of the available series of specimens.

adult proportions are to be considered more important than juvenile, the latter have been included to show ontogenetic trends in this characteristic. Again the comparisons have been made on a basis of equal body lengths B, rather than lengths over-all, L, since this seems a more logical procedure. As previously mentioned, the standard adult lengths represent large, but by no means exceptional adults, as determined from the material at hand. If one sex reaches a distinctly greater length than the other, the standard body length is based on the smaller, so that in no case are tail lengths deduced for body sizes greater than those attained in nature.

TABLE 14

Sexual Dimorphism in Tail Length of Analytic Series
(Expressed as a Percentage in Terms of the
Coefficient of Divergence)

	Juvenile	Adult
Lichanura r. roseofusca	−1.1	9.8
Adelphicos q. sargii	21.6	30.0
Geophis brachycephala	5.7	20.6
Geophis nasalis	14.8	27.8
Diadophis a. similis	14.9	18.7
Diadophis p. arnyi I	25.6	23.1
Diadophis p. arnyi II	18.7	25.7
Boaedon l. lineatus I	34.8	39.2
Boaedon l. lineatus II	24.3	34.7
Masticophis f. piceus	−7.7	−1.4
Masticophis lateralis	−0.8	3.8
Salvadora g. virgultea	3.2	3.6
Phyllorhynchus b. browni	46.3	58.3
Phyllorhynchus d. nubilus	36.4	62.9
Phyllorhynchus d. perkinsi I	27.8	48.5
Phyllorhynchus d. perkinsi II	22.6	48.8
Arizona e. occidentalis I	22.6	6.9
Arizona e. occidentalis II	12.6	9.9
Pituophis c. annectens	10.4	11.8
Pituophis c. deserticola I	12.2	8.2
Pituophis c. deserticola II	21.0	7.9
Lampropeltis g. californiae	8.1	3.9
Rhinocheilus l. lecontei I	12.7	9.9
Rhinocheilus l. lecontei II	16.8	6.6
Rhinocheilus l. clarus	26.7	7.4
Toluca l. lineata I	26.7	37.8
Toluca l. lineata II	27.7	31.5
Toluca l. varians	18.5	32.2
Sonora m. linearis	10.3	18.7
Sonora o. occipitalis	24.8	13.6

TABLE 14

(Continued)

Sexual Dimorphism in Tail Length of Analytic Series
(Expressed as a Percentage in Terms of the
Coefficient of Divergence)

	Juvenile	Adult
Sonora o. annulata	17.1	16.7
Chilomeniscus s. stramineus	24.2	19.0
Thamnophis hammondii	1.2	10.7
Thamnophis o. ordinoides	6.7	17.1
Thamnophis o. biscutatus	10.9	11.6
Conopsis nasus	25.0	27.8
Hypsiglena ochrorhynchus	12.9	19.2
Trimorphodon vandenburghi	11.3	17.4
Tantilla eiseni	27.8	13.8
Elapsoidea niger	31.9	17.3
Micrurus a. mayensis	19.2	32.2
Micrurus n. nigrocinctus	34.9	41.6
Micrurus n. divaricatus	29.7	43.2
Agkistrodon m. mokeson	9.7	4.6
Trimeresurus gramineus	0.2	22.8
Trimeresurus elegans	6.0	16.6
Bothrops insularis	15.1	17.6
Atheris squamigera	12.2	19.6

(Negative values indicate a female tail length greater than the male.)

Sexual dimorphism in the tail length of snakes is so well known that it requires no detailed study to demonstrate its existence. Thus, among the 48 series which were investigated analytically, all but two have a highly significant adult sexual dimorphism, with P less than 0.01; in fact, in all but 4 cases P is less than 0.0001, and this notwithstanding the fact that several of the series contain relatively few specimens.

The four exceptions are: First, *M. f. piceus*, which is the only subspecies with a female tail exceeding the male, although the difference is of doubtful significance ($P = 0.075$); secondly, *S. g. virgultea* ($P = 0.056$) this being the only other series in which the sexual difference is below the usually accepted level of significance ($P = 0.05$); *M. lateralis* ($P = 0.009$), and *R. l. lecontei* ($P = 0.0007$). The two last have a highly significant sexual dimorphism and are mentioned only because they do not reach $P = 0.0001$.

In Tables 15 and 16 I have presented the coefficients of sexual dimorphism of the series which were investigated only graphically. Necessarily these coefficients are somewhat less accurate than those derived analytically.

TABLE 15

Sexual Dimorphism in Tail Length of Graphic Series
(Expressed as a Percentage in Terms of the
Coefficient of Divergence)

	Juvenile	Adult
C. bottae	6.1	33.5
G. semidoliatus	16.9	27.2
N. psephota	13.9	11.7
N. s. morleyi	6.3	30.5
D. a. modestus	3.9	14.5
L. c. ornatum	33.4	22.9
C. c. constrictor	8.0	8.1
C. c. flaviventris	10.7	8.7
C. c. mormon	3.2	8.8
M. f. flagellum	−10.4	3.8
M. f. testaceus	7.6	6.0
M. f. piceus (Cape)	−9.1	−1.0
M. t. taeniatus	−19.3	0.8
P. d. perkinsi (Arizona)	31.4	50.0
E. rufodorsata	25.7	24.3
A. e. elegans	7.0	4.1
P. s. affinis (C. Arizona)	10.9	12.0
P. s. affinis (Yuma)	6.0	11.8
L. multicincta	−9.0	4.3
R. l. lecontei (Arizona)	14.2	8.8
R. l. tessellatus	10.2	6.7
S. episcopa	17.7	19.5
S. m. linearis (not Laguna)	8.9	18.1
N. t. tigrina	9.1	12.8
C. f. punctigularis	18.1	7.8
T. gracilis	8.1	16.0
T. albolabris	17.5	43.7

There is evident a tendency of sexual dimorphism to increase with age; that is, the regression lines of the sexes tend to converge in the juvenile range. But this tendency is by no means universal; out of a total of 88 series, 25, or about 28 per cent, have a contrary trend. This divergence from what might be considered a normal scheme of variation, is particularly evident in certain genera, *Arizona, Pituophis,* and *Rhinocheilus* being conspicuous examples. It might be thought that this juvenile convergence of the lines is due to inaccurate sexing of the juveniles. This may be true to a very minor degree in some series, but there are others, *Phyllorhynchus* for example, in which mistakes in sexing are virtually impossible, yet the same tendency is in evidence.

TABLE 16

Sexual Dimorphism in Tail Length of *Thamnophis*
(Expressed as a Percentage in Terms of the
Coefficient of Divergence)

Species	Locality	Juvenile	Adult
T. o. vagrans	Nevada, Utah	5.2	11.6
T. o. biscutatus	Klamath region	10.9	11.6
T. o. elegans	Lassen, Modoc, Shasta, Plumas Cos.	8.1	12.6
T. o. hydrophila	SW. Oregon	7.5	12.2
T. o. hydrophila	NW. California	7.1	10.7
T. o. couchii	Cromberg, Plumas County	19.5	19.2
T. hammondii	San Diego County	1.2	10.7
T. hammondii	NW. Lower California	−4.7	9.8
T. digueti	Lower California	6.2	9.7
T. o. atratus	NW. California	8.5	13.1
T. o. atratus	San Francisco Bay region	2.9	12.4
T. o. ordinoides	Canada	16.3	20.5
T. o. ordinoides	Washington	5.3	14.8
T. o. ordinoides	Portland	6.7	17.1
T. o. ordinoides	SW. Oregon	11.3	15.9
T. marcianus	Arizona	3.2	11.0

Certain generic tendencies in the adult sexual dimorphism are evident in these tables. *Phyllorhynchus* has the highest dimorphism of the forms investigated. Others outstandingly high are *Micrurus, Toluca, Geophis,* and *Boaedon*. The racers are conspicuously low. These genera with high dimorphism are all short-tailed, while the racers are long-tailed. This at once suggests that there may be a correlation between tail proportions and sexual dimorphism. To investigate this possibility each subspecies was represented by an ordinate determined by the mean between the male and female tail-to-body ratio, while the abscissa was taken as the coefficient of adult sexual divergence.

It is found that there is a rough correlation—long-tailed snakes do tend to have low sexual dimorphism and vice versa. However, the correlation is not particularly close and many species are exceptions, among the most conspicuous being *Lichanura, Arizona, Pituophis, Rhinocheilus, Elapsoidea,* and *Agkistrodon*. All of these are short-tailed snakes, yet they have a low sexual dimorphism. Ignoring these, the regression equation is found to be approximately $S = 56 - 1.33T$, where S is the coefficient of sexual dimorphism in percent, while T is the mean adult tail proportionality, that is, the mean between the sexes at standard adult body length. A somewhat better fit is given by the parabola $S = 78.76 - 3.15T + 0.031T^2$. But it should be emphasized that the relationship is only approximate; while the correlation is not to be questioned, many species do not fall close to either of these lines.

This relationship is not entirely unexpected. In the short-tailed snakes the male sex organs would require a certain minimum space which would tend to increase dimorphism. On the other hand, the long-tailed snakes, in which the tails serve various useful purposes, such as for balance, propulsion, holding, or climbing, the necessity for the space for primary sex organs would obviously have a more incidental effect on tail length.

Rattlesnake Tail Proportionalities

The rattlesnakes, with their relatively short tails, do not comprise a particularly fruitful field for the study of tail proportionalities. However, sexual dimorphism is considerable, and there is some interspecific variation. I shall therefore make a survey of the rattlesnake data. This section of the tail-length study is to be considered the appropriate tail-length chapter of the series of papers I have hitherto published under the general title of "A Statistical Study of the Rattlesnakes".[31]

In determining the tail length of a rattler, the measurement is made from the center of the anal plate to the anterior edge of the proximal rattle. Specimens with incomplete tails are few. On the whole, the rattlesnake material, in many species, is fairly adequate. As all correlations are high and tail lengths are usually less than 10 per cent of body length, I shall neglect the matter of spurious correlation and use L rather than B as a basis for all calculations. Therefore, the regression equations, if they prove to be linear, will be expressed in the form $T = a + bL$.

As an initial approach it may be of interest to neglect ontogenetic variation and determine the mean and dispersion of the tail proportionality, using the tail ratios of the individual specimens as the variates, a method not employed in the study of the other snakes. The results of such calculations, of obviously limited utility owing to the probable effects of the ontogenetic distribution of the samples, are presented in Table 17. For this reason the coefficients of variation V are to be considered of more value than the mean ratios. Not all of the series are territorially homogeneous.

A substantial sexual dimorphism will be noted. Variability tends to be higher among females than males. Specific differences in proportionality are evident, but not so great as those found within genera of colubrids, where the tails have many functions quite different from that of a rattle vibrator.

Having made this preliminary survey, I now proceed to an investigation of the rattlers by the methods previously employed with the colubrids, first testing a few series analytically, then making graphic determinations on other less adequate series.

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[31] Occ. Papers S. D. Soc. Nat. Hist., Nos. 1, 3, 4, 5, 6.

TABLE 17

Dispersions of the Tail Length to Length Over-all Ratio in *Crotalus*
(Neglecting Ontogenetic Variation)

Species	Territory	Males			Females		
		N	M	V	N	M	V
C. cinereous ....Texas-Arizona		247	0.0768	6.16	186	0.0593	9.67
C. ruber .... San Diego Co.		79	0.0687	5.66	81	0.0539	11.80
C. s. scutulatus........All		160	0.0730	7.10	93	0.0543	11.74
C. v. viridis............Pierre		143	0.0745	5.50	151	0.0547	8.66
C. v. viridis............Platteville		453	0.0742	6.23	387	0.0536	9.70
C. v. lutosus............All		146	0.0707	6.88	103	0.0558	9.26
C. v. oreganus..........San Diego Co.		137	0.0740	7.19	135	0.0599	9.55
C. cerastes................All		101	0.0853	7.09	74	0.0620	10.46

N is the number of specimens, M the mean of the ratios calculated
separately, and V the coefficient of variation of the ratios in per cent.

From both the analytic and graphic studies, linearity of regression is
again evident among the rattlers, as it was in the other genera. Six of the
largest series were tested for linearity by an F-test.[32] A probable departure
from a straight line was found in only one (*ruber* females). In the interest
of simplicity in the treatment of difference problems we are fully justified
in the assumption of linearity throughout.

Table 18 presents an analytical study of seven large, territorially homo-
geneous series of rattlers. Comparing the results with those found in the
taper-tailed snakes previously discussed, we find that the correlation co-
efficient, *r*, tends to be somewhat lower in the rattlers. Of course, as the
rattlers have short tails, the values of *b* in the regression equation
$T = a + bL$ are lower than in most other snakes. But the greatest differ-
ence lies in the values of *a;* these are low in the rattlers, thus indicating
a reduced ontogenetic variation. In fact, *a* is found to be significantly dif-
ferent from zero in only three out of 14 cases, all three being females.
Hence, to ignore the change in tail proportionality with age would not
be as serious in rattlesnake investigations as in most other genera. The
variability of tail proportionality in the rattlers is high as compared to
most colubrids, as shown by the mean coefficient of variation (compare
with Table 5). Sexual dimorphism, as indicated by the coefficient of
divergence between adult males and females, is high, as is to be expected
in short-tailed snakes, although not reaching the differences attained by
some colubrids (compare with Table 14).

[32] The modern test for linearity will be found in most recent statistical texts, as for
example: Rider, 1939, p. 130; Yule and Kendall, 1937, p. 455; Goulden, 1939, p. 211.
I find it desirable to omit Sheppard's correction in the *r* computations, if a linearity test
is to be made.

TABLE 18

Relationship of Tail Length to Length Over-all in Rattlesnakes

(Analytic Series)

Item	Cincreous Arizona		Lucasensis Cape Region		Ruber San Diego Co.		Viridis Pierre		Viridis Platteville		Oreganus Pateros		Oreganus San Diego Co.	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Number of Specimen, N	87	95	161	140	156	104	364	342	452	392	314	266	354	354
Coefficient of correlation, r	.968	.959	.939	.935	.986	.974	.985	.959	.978	.954	.962	.942	.982	.962
Regression coefficient, b	.0769	.0560	.0720	.0522	.0692	.0514	.0740	.0496	.0725	.0476	.0736	.0562	.0730	.0524
Regression constant, a	−1.279	1.568	1.039	1.336	−.582	.720	.430	2.618	.791	2.952	−.111	.340	.659	2.957
Significance of a, P_a	.50	.24	.63	.37	.37	.36	.38	.0001−	.091	.0001−	.88	.62	.078	.0001−
Standard error of estimate	5.119	3.552	4.294	3.172	3.298	2.926	2.925	2.974	3.251	2.764	3.203	2.484	2.783	2.266
Mean coefficient of variation, V, per cent	8.01	8.25	5.72	6.82	6.57	9.01	5.86	8.43	7.30	9.17	7.02	8.11	8.23	9.24
Standard adult length over-all, SL, in mm.	1200	1200	1050	1050	1100	1100	950	950	850	850	850	850	950	950
Tail-length ratio at SL	.0758	.0573	.0730	.0534	.0686	.0521	.0745	.0523	.0735	.0510	.0735	.0566	.0737	.0555
Coefficient of sexual divergence at SL	27.76		30.96		27.43		34.96		36.02		25.97		28.19	

As before, it is found that the proportionate dispersion about the re-
gression line remains substantially constant throughout life. The follow-
ing results, for example, were derived from a study of restricted size
groups of the Platteville series, *C. v. viridis*:

	Coefficient of Variation, Per Cent	
	Males	Females
Juveniles	6.19	7.38
Adults	6.16	8.30

It will be seen that there is no evidence of a decrease in the coefficient
of variation with increased size, such as would be the case if the dispersion
about the regression line remained constant in dimension rather than pro-
portion. In general, we find the same conditions to exist in *Crotalus* as the
other genera: Ontogenetic change in tail proportionality (of reduced im-
portance, however); linearity of regression; and a constant coefficient of
variation through life.

Table 19 contains the results of graphic studies on the other series of
rattlers available to me. The data on the analytic series have been repeated
to render comparisons easier. Where a territorially restricted series has
been at hand I have used it to represent its species, thus avoiding the possi-
bility of intrasubspecific variability. But often I have had to go farther
afield and have used all available specimens to secure enough points for a
trend line. In many of the rarer forms the material is too inadequate to
be trustworthy. Some series are poorly distributed ontogenetically, lack-
ing either juveniles or adults. Altogether, I believe the values of b are
moderately reliable, those of a not very dependable. In general, while
we may draw the conclusion that the ontogenetic change in the rattlers is
less important than in most colubrids, it still is worthy of some attention.
If we average all values of a we find the mean of the males to be -0.5,
and of the females $+1.1$. I think we may conclude that male tail ratios in-
crease slightly with age, while female tail proportionalities decrease some-
what more, and that a values of -0.5 in the case of the males and $+1.1$
in the females probably indicate a situation approximated in most species.
To give an idea of the extent of ontogenetic change thereby involved,
these average values of a are applied to a hypothetical species 300 mm.
long at birth and 1000 mm. at maturity, with b values (close to *cinereous*
or *viridis*) of 0.075 for the males and 0.055 for the females. The results
follow:

	Males	Females	Sexual divergence per cent
Tail ratio at birth	0.0733	0.0587	22.2
Adult tail ratio	0.0745	0.0561	28.2
Ontogenetic divergence, per cent	1.6	-4.5	

TABLE 19
Relationship of Tail Length to Length Over-all in Rattlesnakes
(General Series)

Species or Subspecies	Area or Series	Number of Specimens M	F	Regression Coefficient, b M	F	Regression Constant, a M	F	Standard Adult Length Over-all mm.	Ratio of Tail Length to Length Over-all at Standard Adult Length M	F	Adult Coefficient of Sexual Divergence, Per Cent
C. durissus durissus	All	29	22	.1030	.0684	− 4.0	1.0	1450	.1002	.0691	36.7
C. durissus terrificus	All	31	34	.1006	.0669	− 1.9	0.7	1150	.0989	.0675	37.8
C. unicolor	All	8	5	.1042	.0677	− 1.5	2.7	800	.1023	.0711	36.0
C. basiliscus	All	68	46	.0927	.0644	− 2.1	1.7	1450	.0913	.0652	33.4
C. enyo	All	34	21	.0944	.0629	0.6	1.2	750	.0952	.0645	38.4
C. molossus molossus	All	90	56	.0725	.0532	− 1.0	3.1	1000	.0715	.0563	23.8
C. molossus nigrescens	All	62	56	.0757	.0560	0.3	2.5	1000	.0760	.0585	26.0
C. adamanteus	All	31	43	.0830	.0619	0.7	1.1	1700	.0834	.0625	28.7
C. cinereous	Texas and Oklahoma	149	124	.0808	.0578	− 1.5	1.6	1450	.0798	.0588	30.3
C. cinereous	Arizona	87	95	.0769	.0560	− 1.3	1.6	1200	.0758	.0573	27.8
C. cinereous	California	42	29	.0810	.0585	− 1.8	− 0.3	1200	.0795	.0582	30.9
C. tortugensis	All	30	17	.0790	.0588	− 3.4	− 0.8	850	.0750	.0579	25.8
C. lucasensis	Cape Region, B. C.	161	140	.0720	.0522	1.0	1.3	1050	.0730	.0534	31.0
C. ruber	San Diego Co.	156	104	.0692	.0514	− 0.6	0.7	1100	.0686	.0521	27.4
C. exsul	All	17	7	.0707	.0520	− 1.0	1.5	800	.0694	.0539	25.1
C. scutulatus scutulatus	Arizona	156	97	.0746	.0503	− 0.6	2.2	950	.0740	.0526	33.8
C. scutulatus scutulatus	California	84	52	.0742	.0536	− 0.5	0.6	950	.0737	.0542	30.5
C. viridis viridis	Montana	80	93	.0730	.0485	1.8	3.5	1000	.0748	.0520	36.0
C. viridis viridis	Pierre, S. D.	364	342	.0740	.0496	0.4	2.6	950	.0745	.0523	35.0
C. viridis viridis	Platteville, Colo.	452	392	.0725	.0476	0.8	3.0	850	.0735	.0510	36.0
C. viridis viridis	New Mexico	84	53	.0772	.0560	0.9	1.7	800	.0783	.0581	29.6
C. viridis nuntius	Winslow	69	37	.0751	.0504	1.1	2.7	550	.0771	.0553	32.9
C. viridis abyssus	All	13	9	.0722	.0590	1.0	− 0.2	850	.0734	.0588	22.1
C. viridis lutosus	Utah	84	58	.0697	.0522	1.0	2.1	950	.0708	.0544	26.2
C. viridis lutosus	Nevada	52	33	.0737	.0556	− 0.9	0.9	950	.0728	.0565	25.2
C. viridis decolor	All	19	19	.0803	.0591	− 1.4	0.0	650	.0781	.0591	27.7
C. viridis oreganus	Pateros, Wash.	314	266	.0736	.0562	− 0.1	0.3	850	.0735	.0566	26.0
C. viridis oreganus	San Diego Co.	354	354	.0730	.0524	0.7	3.0	950	.0737	.0555	28.2
C. viridis oreganus	Arizona	51	22	.0679	.0520	1.1	1.8	850	.0692	.0541	24.5
C. mitchellii mitchellii	Cape Region, B. C.	50	30	.0849	.0676	− 2.4	− 3.0	800	.0819	.0638	24.9
C. mitchellii pyrrhus	San Diego Co.	68	34	.0743	.0578	− 1.8	0.2	950	.0724	.0580	22.1
C. mitchellii pyrrhus	Arizona	28	13	.0698	.0606	2.2	0.2	900	.0722	.0608	17.1
C. mitchellii stephensi	All	67	42	.0823	.0592	− 1.2	0.6	750	.0807	.0600	29.4
C. tigris	All	28	13	.0861	.0621	− 2.2	2.0	700	.0830	.0650	24.3
C. cerastes	Arizona	52	28	.0886	.0624	− 2.1	− 0.8	600	.0851	.0611	32.8
C. cerastes	Nevada and Utah	10	7	.0998	.0698	− 3.1	− 1.7	600	.0946	.0670	34.1
C. cerastes	Colorado Desert	134	114	.0932	.0655	− 3.9	− 1.3	600	.0867	.0633	31.2
C. cerastes	Mohave Desert	101	55	.1017	.0660	− 3.8	− 0.4	600	.0954	.0653	37.4
C. polystictus	All	9	8	.0763	.0578	2.5	0.5	800	.0794	.0584	30.5
C. horridus horridus	All	43	69	.0766	.0570	0.6	1.8	1050	.0772	.0587	27.3
C. horridus atricaudatus	All	13	28	.0763	.0608	1.5	1.0	1250	.0775	.0616	22.9
C. lepidus lepidus	All	16	5	.0850	.0713	0.2	0.2	550	.0854	.0717	17.4
C. lepidus klauberi	Arizona	53	50	.0807	.0655	1.8	2.4	560	.0839	.0698	18.4
C. triseriatus triseriatus	All	38	39	.0963	.0705	0.2	1.5	530	.0967	.0733	27.5
C. triseriatus pricei	All	39	20	.0893	.0727	− 0.8	0.2	530	.0878	.0731	18.3
C. willardi	All	16	14	.1023	.0820	0.6	3.8	475	.1036	.0900	14.1
S. ravus	All	11	7	.0967	.0818	− 0.4	− 0.4	520	.0959	.0810	16.9
S. miliarius miliarius	All	36	20	.1180	.0958	0.7	1.0	450	.1196	.0980	19.9
S. miliarius barbouri	All	103	80	.1202	.1034	1.7	1.2	535	.1234	.1056	15.5
S. miliarius streckeri	All	55	49	.1276	.1060	− 0.4	2.1	520	.1268	.1100	15.6
S. catenatus catenatus	All	177	170	.1065	.0780	− 0.7	1.8	700	.1055	.0806	26.8
S. catenatus tergeminus	All	43	65	.1109	.0837	− 0.7	0.4	680	.1099	.0843	26.4

An ontogenetic difference of 4.5 per cent from birth to maturity is present in the females. It will be observed that sexual dimorphism increases with age to a considerable degree; this results from the divergence of the two regression lines inherent in the negative value of a in the male line, whereas it is positive in the female.

In assigning standard adult lengths over-all, I have taken as a guide large, but not record-breaking, sizes attained by the smaller sex—the females in all species except *cerastes*.

Some racial trends of interest will be noted in Table 19. It will be seen that the males of many species have a tail ratio of between 0.07 and 0.08, while most females fall between 0.05 and 0.06. These figures may be considered to represent the rattlesnake mode; they are characteristic, for example, of the *cinereous* and *viridis* groups. *Durissus* and its allies (including *enyo*) are definitely long-tailed, as is *adamanteus* to a lesser degree. *Stephensi*, *tigris*, and *cerastes* are moderately long-tailed; this is also the case with the smaller rattlers, *lepidus*, *triseriatus*, and *willardi*. Small species are generally long-tailed. All members of the genus *Sistrurus* are long-tailed, especially *miliarius*, which also has a low sexual divergence. The shortest-tailed species is probably *ruber*.

It is to be regretted that sufficient specimens of the interesting form *stejnegeri*, the longest-tailed member of the genus *Crotalus*, were not available to permit ascertaining its regression lines. Three males have an average tail proportionality of 0.1209, thus approximating the tail ratio of *miliarius*. Other forms, of which only a few specimens were available, are the following:

> 3 female *totonacus* average 0.681
> 1 male *vegrandis* 0.1010; 1 female 0.0705
> 1 male *omiltemanus* 0.0868; 2 females 0.0682

Tail length is sometimes useful as a diagnostic character. The most important case among the rattlers is the differentiation of *basiliscus* from *molossus*. These two species have a considerable superficial similarity. There is some difference in tail proportionality, especially in the males, for *basiliscus* belongs to the long-tailed *durissus* group, while *molossus* is more normal. The easiest way to diagnose questionable specimens is to make a graphic determination by drawing the regression lines of the two species (the sexes must be handled separately), using the coefficients a and b in Table 19; then plot the positions of the doubtful specimens, allocating each to whichever species it more nearly approaches. This should give a correct determination in most cases. Of course, other characters, especially those of pattern, should be used to confirm the diagnosis.

This brings up a problem of some interest which may be solved analytically: What is the overlap in the *molossus* and *basiliscus* tail-length ranges? As the regression lines are not parallel, there is a slightly different

answer for every snake-length over-all. I shall use, as an example, male snakes of 1000 mm.; normal dispersion about the regression line is assumed, as well as an 8 per cent coefficient of variation, which is a fair average among the rattlers. From the regression line we calculate the mean tail-length of *basiliscus* at 1000 mm. to be 90.6 mm., with a standard deviation (8 per cent) of 7.248 mm.; the corresponding figures for *molossus* are 71.5 mm. and 5.720 mm. The difference between the means, d, is 19.1 mm. The ratio between the standard deviations, placing the larger in the numerator, is assigned the symbol k; in this case it equals 1.267. The equation for the point of intersection between two normal curves (which also defines the minimum overlapping areas) is found to be

$$x = \frac{-d + [k^2 d^2 + 2\sigma_2^2 (k^2 - 1) \log_e k]^{1/2}}{k^2 - 1}$$

where σ_2 is the larger of the two standard deviations. Solving this we find that 6.92 per cent of the *molossus* would fall in the *basiliscus* area and 7.13 per cent of the latter in the area of the former; that is, these figures represent the tails of the curves beyond their point of intersection. This gives an idea of the number of specimens which would be incorrectly identified by the use of this criterion.

I should call attention to the fact that the same method of analysis may be used to determine the percentage of specimens of any species which would be incorrectly sexed by the use of tail length alone. Of course, I do not suggest this as a practical method. Rather, it may be recommended that the available specimens be plotted graphically. Aberrants and doubtful specimens will be clearly apparent, and should be rechecked. In fact, one can, if he wishes, draw a straight line which seems best to separate the sexes; the equation of this line is then determined and may thereafter be employed as a guide in rechecking the sexing. For example, I find that the line $T = 0.786L - 2.0$ separates the sexes in the Colorado Desert specimens of *C. cerastes* quite consistently, few specimens of either sex straying to the wrong side of the line. Thus, I know that a specimen 500 mm. long with a tail less than 37.3 mm. long is quite unlikely to be a male and, if so recorded, should be rechecked. This may appear complicated when the equation is cited, but it is rapid and simple, once the specimens have been plotted on cross-section paper.

ACKNOWLEDGMENTS

in preparation of his 1940 monograph. Mr. Joseph R. Slevin worked with me for a number of days measuring specimens in the fine collection of the California Academy of Sciences. To Mr. Charles E. Shaw I am much indebted for the measurements of most of the series of snakes contained in my own collection. As usual, I have had the advantage of the pertinent criticisms of Mr. C. B. Perkins of the Zoological Society of San Diego. The diagram was prepared by Mr. L. C. Kobler, who likewise prepared the figures for the succeeding paper.

SUMMARY AND CONCLUSIONS

1. Various statistical equations defining the relationship of parts and wholes are given.

2. The coefficient of divergence is defined and its standard error is presented.

3. The quantitative effects of spurious correlation are discussed.

4. Examples of the use of the coefficient of divergence, both as a measure of sexual dimorphism in scalation, and of racial difference are presented.

5. Methods and precautions necessary in accumulating data on the tail-lengths of snakes are cited. Graphic and analytic methods of determining trends and dispersions are discussed. The importance of the graphical method in eliminating errors and aberrants is pointed out.

6. The tail-length proportionalities of 48 series of snakes are analyzed, together with 40 others which are treated graphically. The statistics are set forth. The relationship between tail length and body length, or length over-all, is linear, or substantially so, in every species studied. An ontogenetic variation in tail proportionality of considerable extent is usually present, so if the tail length is to be used in taxonomic problems, provision must be made for this variation or the results may be seriously in error. The dispersion of individual specimens about the regression line remains substantially constant in proportion (rather than in absolute measure) during life.

7. Ontogenetic trends differ in the various genera and species. Often there is a tendency toward an increase in tail proportionality with age, especially in the males, but some forms show contrary effects. *Phyllorhynchus* is a genus of high ontogenetic change.

8. Parabolic tail-length equations are deduced for a few species. However, as they seem to have no advantage in accuracy, the simpler straight-line equations are to be preferred in taxonomic studies.

9. There is a negative correlation between tail proportionality and body thickness—slim snakes tend to have long tails; however, the correlation is not particularly close.

10.   Methods of determining the significance of differences, taking into account both ontogenetic change in proportionality, and dispersion about the regression lines, are evolved. Example problems are presented.

11.   The sexual dimorphism in tail proportions of a number of species and subspecies are stated in terms of the coefficient of divergence. There is a tendency of sexual dimorphism to increase with age, but this is not universal. There is a moderate correlation between sexual dimorphism and tail ratio, short-tailed snakes having a higher sex difference, but there are exceptions to the rule.

12.   Similar methods were employed in a study of rattlesnake tail lengths. The same trends are disclosed as in the snakes with tapered tails, although the ontogenetic change is reduced. Some boundary problems are analyzed.

The question naturally arises as to how far the methods herein outlined are applicable to ordinary taxonomic problems.

The purpose of this paper has been dual: To determine the nature of the tail-length proportion in such series of snakes as are available, to see if there are any standardized modes of variation; and, to suggest statistical methods for the use of the tail-length proportion in taxonomy.

Probably the most important conclusion, insofar as ordinary studies are concerned, is that the tail-length ratio is usually not ontogenetically constant. Such being the case, if interspecific comparisons are to be made, it is essential that either statistical methods, along the lines suggested herein, be employed, or else the material used in the differential studies be limited to specimens within a narrow range of age, adults preferred. The most serious errors will occur if two series are compared, in one of which juveniles predominate, while the other is made up largely of adults. With these precautions, and having in mind the limited material available in most taxonomic problems, it will be sufficiently accurate to employ as the variates, the calculated ratios of the several specimens, using the formulas for the significance of the difference between two means. But in monographic work, with plenty of material available, the more thorough methods are to be recommended; at least they should be employed with one or two of the largest homogeneous series, to determine the nature of the variation of tail length within the genus. The analytic method will be found particularly useful in the study of subspecies and races, but even then it is only valuable when relatively large series are at hand. Graphic studies, because of the clarity with which they disclose aberrants, mis-identifications, and errors of sexing or measurement, are to be recommended in all cases where tail length is to be used as an identifying character, and particularly when it is to be employed in differential diagnosis.

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